Strategies for success: Copepods in a seasonal world

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Publication date:
2014

Document Version
Publisher's PDF, also known as Version of record

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DTU

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PhD Thesis

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Defence 8 April 2014

DTU Aqua
National Institute of Aquatic Resources

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February 2014

Technical University of Denmark
National Institute of Aquatic Resources
February 14, 2014

Popular abstract

Climate change is expected to threaten biodiversity, partly due to rising temperatures and through an increase in the variability of weather patterns. Species must adapt to new conditions and on the individual level, the ability of an organism to defend itself against predators and invasive (foreign) species is affected where its environment is changing. In this context, mathematical and simulation models are invaluable tools for providing a deeper understanding of the organism's flexible responses to a single or multiple stressors. They can then be used to predict and assess the ecosystem future, and allow for management plans. Copepods, the so-called "fleas of the sea", are an important link between the algal production and larger species such as fish, sea birds and ever whales. The diversity of copepod species is a particularly interesting case study as these species have developed a wide range of strategies which has allowed their dominance across many different habitat types. At high latitudes, they have adapted to the long winter by entering hibernation, sometimes down to thousands of meters below the surface. They return in the spring to feed, reproduce, and prepare for the next winter. At the surface, they face daily obstacles: while attempting to grow and breed, they must also avoid predators. Daily migration to deeper water during day-time has been shown to be a successful trade-off between feeding sufficiently and avoiding visual predators when they are the most efficient (i.e. during daylight). This daily vertical migration emerges from a game between prey and predators where the increased risk by visual predators counterbalances the need for feeding during day-time. Similar behaviors can be observed, and show considerable variability between and within species, some of which can be explained by individual size. Individual vertical migration has implications, for example, in the carbon removal from the surface toward the deep ocean, where it is trapped. Thus animal behavior should be included in large models following the fate of the carbon released in the atmosphere. Reproduction timing is also a key element of species success in a given environment. The range of breeding strategies is wide, but one of the most fascinating traits is how individuals should allocate their resource to reproduction. Similar to "the grasshopper and the ant" fairytale of Jean de Lafontaine, individuals can either rely entirely on food availability to produce eggs (strategy called income breeding - the

grasshopper's strategy) or store reserves to spawn at some later date (capital breeding - the ant's strategy). Income breeding secures immediate offspring production and allows for multiple generations a year; a strategy particularly successful in long feeding seasons. Capital breeders on the other hand, can spawn at a time suitable for their offspring, ensuring the young better chance of survival, although the parents take a bet on their own survival until egg laying. This strategy is preferential when the productive season is short as the offspring can benefit from the full duration of the feeding season before facing the harsh winter. While daily vertical migration is a flexible answer to a current situation, breeding strategy is inherited and shapes the species success in their environment. For example, income breeding allows for a fast population growth in long feeding season, but is very vulnerable to "bad" years. Capital breeders seem more robust to inter-annual variation, but does not have the capacity for fast population expansion. Thus, within populations, trade-offs in behavior and life-history strategy provide valuable insights into the species capacity to cope with environmental changes, and help access the fate of these populations under the threat of climate change.

Populærresumé

Det er forventet at klimaforandringer ændrer biodiversiteten, dels på grund af forhøjede temperaturer, dels på grund af variabilitet i vejrets mønstre. En organisme må tilpasse sig på det individuelle plan, og dens evne til at forsvare sig mod rovdyr og invasive (fremmede) arter, påvirkes når miljøet ændres. I denne kontekst er matematiske modeller uvurderlige redskaber, da de giver en dybere forståelse af en organismes fleksible responser til en enkelt eller flere stressfaktorer. Modellerne kan derefter bruges til at forudsige og vurdere økosystemets fremtid og derefter fastsætte en forvaltningsplan. Vandlopperne er et vigtigt led mellem planteplankton produktionen og højere trofiske niveauer som dyreplankton, fisk, havfugle og også hvaler. Deres diversitet er et særligt interessant casestudie, da disse arter har udviklet en lang række strategier, der har gjort dem til dominante arter i flere forskellige habitattyper. På høje breddegrader har de tilpasset sig til den lange vinter ved at gå i hi, nogen gange på op til 1000 meters dybde. Til foråret vender de tilbage til overfladen for at æde, reproducere sig og forberede sig til den næste vinter. Mens de er ved overfladen, står de overfor mange udfordringer: mens de forsøger at vokse og gyde skal de undgå at blive spist. Daglig migration til dybere vandlag i løbet af dagen, har vist sig at være en succesfuld afvejning mellem at få tilstrækkeligt føde, og samtidig undgå visuelle rovdyr når de er mest effektive (dvs. i dagslys). Denne daglige vertikale migration kommer fra et spil mellem rovdyr og byttedyr, hvor den forhøjede risiko for visuelle rovdyr opvejer behøvet for at spise i løbet af dagen. Lignende adfærd kan man observere, og den viser stor variabilitet mellem og indenfor arter noget som kan forklares af individuel størrelse. Individuel vertikal migrering har betydning for, f.eks., fjernelse af kulstof fra overfladevandet til dybhavet, hvor det bliver fanget. Derfor skal dyrenes adfærd inkluderes i store modeller der følger kulstoffets vej igennem atmosfæren. Gydetidspunktet er også et nøgleelement for arters succes i et givent miljø. Udbredelsen af gydestrategier er stor, men et af de mest fascinerende træk er hvordan individer skal allokere deres ressourcer til reproduktion. I lighed med eventyret om "græshoppen og myren" af Jean de Lafontaine, kan individer være afhængige af enten fødetilgængelighed for at lægge æg (en strategi der hedder indkomstgydning græshoppens strategi), eller at gemme et forråd for at gyde på et senere tidspunkt (kapitalgydning

myrens strategi). Indkomstgydning sikrer en umiddelbart produktion af afkom, og tillader flere generationer om året; en strategi der er særligt god når sæsonen for mad er lang. Kapitalgydere, på den anden side, kan gyde på et tidspunkt der er tilpasset deres afkom, hvilket sikrer afkommet bedre mulighed for at overleve, selvom forældre risikerer deres egen overlevelse indtil æggene er gydt. Denne strategi er at foretrække når den produktive sæson er kort, da afkommet kan få udbytte af den fulde længde af sæsonen for mad før de skal imødekomme den barske vinter. Imens daglig vertikal migration er et umiddelbart respons til den givne situation, er gydestrategi nedarvet og former arternes succes i deres omkringliggende miljø. Indkomstgyding tillader f.eks. hurtig populationsvækst i en lang fødesæson, men er meget sårbart overfor dårlige år. Kapitalgydere forekommer mere robuste overfor årlig variation, men de har ikke kapaciteten til hurtig populationsvækst. Derfor er afvejninger mellem adfærd og livshistoriestrategier vigtig indsigt i arters mulighed for at overkomme miljømæssige forandringer, og hjælper os til at undersøge deres skæbne overfor truende klimaforandringer.

Summary

Amongst the zooplankton community, copepods display complex and diverse life history strategies, which could explain their wide success in the world ocean. Specifically, in temperate and high latitude ecosystems, copepods are subject to "boom and bust" conditions where annual cycles are punctuated by a short, productive spring blooms, but with relatively little food and harsh conditions for the rest of the year. Due to their world-wide dominance in biomass, and their importance in the food webs, copepods are fairly well studied. However, the success of their complex life-history strategies remain open scientific questions, in particular, how these are attuned to environmental conditions, and how these may be compromised by climate change. Due to their ability to concentrate lipids in their small bodies, copepods are indeed of great ecological significance as they are an important link between phytoplankton production and higher trophic levels such as fish, seas-birds and marine mammals. Their most striking life-history trait includes multiple moulting from egg to adult stages (energetically costly but allowing them to have the most efficient shape to swim relative to their size in water), overwintering at great depth and plastic behaviors such as switching between feeding modes and daily vertical migration allowing them to quickly adapt to local conditions. Some of their life history traits also vary widely amongst species, including how resources are allocated to reproduction and size at maturity. This thesis covers two of these life-history traits: diel vertical migration and the allocation of resource to reproduction.

Diel vertical migration (DVM) strategies arise from a trade-off between feeding and predation risk – both of which tend to be maximized in the surface ocean. The latter is modulated on a day night cycle as the efficiency of visual predators varies with ambient light. An efficient strategy is thus to migrate vertically, feeding at the surface at night, and taking refuge at depth during the day. The first part of this thesis treats DVM with some observations and models. A first study, made from a video plankton recorder in the West coast of Greenland, shows the wide range of migration patterns adopted in the zooplankton community but also within the *Calanus* copepods taxa (chapter 2). A second study shows the emergence of the DVM strategy in a game theory approach, not only of the organism, but also their predator (chapter 3). In addition to controlling trophic transfer in marine

ecosystems, DVM also plays a potential role biogeochemistry of the worlds oceans. A simple modeling method taking behavior into account in large models is therefore needed, as ocean system model are already computationally intensive. The third study investigates how well a simple (myopic) optimization of DVM compares with life-history optimization using dynamic programming (chapter 4). The myopic optimizations shows surprisingly accurate predictive power over a large range of parameter space.

Inspired by the copepods *Calanus finmarchicus* and *C. hyperboreus*, an individual based model is used to study the success of their reproduction strategy as a function of the feeding season duration. The first of these two species is close to an income breeder, relying only on the incoming food supply, while the latter is a capital breeder, storing reserves to spawn at a time not directly dictated by food availability. Although from the same genus, their size at maturity and their distributions differ dramatically. Including behavior and energetic allocation, we thus investigate the effect of the resource allocation trait to reproduction coupled with the most suited maturity size as a function of the feeding season duration (chapter 5). Capital breeding favors large maturity size and is successful in short blooms, while the income breeders are favored in long blooms and benefit from small size. As the output fitness curve functions seem fairly standard, the model is simplified to an analytical approach that is used to investigate the same problem and gives similar results. The closed solutions are then used to explore the parameter space and the resulting pattern is shown to be robust (chapter 6).

This thesis therefore focuses on two main aspects of the life-history of copepods: diel vertical migration and reproduction strategy. The results may be generalized and applied to other species living in a seasonal environment.

Dansk Resumé

I dyreplanktonsamfund viser vandlopper komplekse og diverse livshistorietræk, noget der kunne forklare deres store succes in verdenshavene. Særligt i tempererede systemer på høje breddegrader er vandlopperne udsat for "knald og fald" forhold, hvor årlige cyklusser bliver afbrudt af en korte, produktive forårsopblomstringer og derefter relativt lidt mad og strenge leveforhold resten af året. På grund af vandloppers verdensomspændende biomasse dominans, og deres betydning for havets fødenet, er vandlopper godt undersøgt. Hvorledes vandloppers succesfulde livshistoriestrategi er tilpasset til miljømæssige forhold, og hvordan klimaændringer kan ændre disse, er fortsat åbne videnskabelige spørgsmål. Vandlopper har, på grund af deres evne til at koncentrere fedtstoffer in deres små kroppe, en signifikant økologisk rolle, da de er et vigtigt led mellem planteplankton produktionen og højere trofiske niveauer, som fisk, havfugle og marine pattedyr. Deres mest påfaldende livshistorietræk inkluderer at vokse fra æg til voksne stadier (energetisk dyrt, men det tillader dem at have den mest effektive svømmeform, i forhold til deres størrelse i vandet), at overvintre på store dybder, plastiske træk som at skifte mellem fødemodaliteter og daglig vertikal migration, der tillader dem hurtigt at tilpasse sig til lokale forhold. Nogle af deres livshistorietræk varierer også betydeligt inden for arterne. Det inkluderer hvordan ressourcer bliver allokeret til reproduktion og størrelse ved gydemodenhed. Denne afhandling dækker to af disse livshistorietræk: daglig vertikal migration og allokation af ressourcer til reproduktion.

Daglig vertikal migration (DVM) strategier opstår af et trade-off mellem at spise eller at blive spist to ting der når sit højeste ved havets overflade. At blive spist skifter dog med dag og nat cyklusser, da visuelle rovdyrs effektivitet afhænger af det omgivende lys. Det er derfor en effektiv strategi at migrere vertikalt, hvormed det er muligt at spise ved overfladen om natten, og søge ly på større dybder om dagen. Den første del af denne afhandling behandler DVM med observationer og modeller. Det første studie, der er lavet ved hjælp af en video plankton optager på Grønlands vestkyst, viser at der er stor adspredelse af migrationsmønstre i dyreplanktonsamfundet, men også inden for *Calanus* familien (kapital 2). Et andet studie viser hvordan DVM strategien opstår ud fra spilteori, ikke kun for organismen, men også for dens rovdyr (kapitel 3). Ud over at kontrollere den trofiske transfer i ma-

rine økosystemer, spiller DVM også en vigtig potentiel rolle i verdenshavenes biogeokemi. Det tredje studie undersøger hvordan simpel ("snæversynet") optimering af DVM kan sammenlignes med livshistorieoptimering ved at bruge dynamisk programmering (Kapitel 4). Dette giver muligheden for at simulere DVM effekter in store ocean modeller. "Snæversynede" optimeringer viser overraskende præcis forudsigende kraft over store intervaller i parameterrummet.

For at studere succesen af vandloppers reproduktionsstrategi, som en funktion af føde-sæsonens længde, bruges en individ-baseret model, inspireret af vandlopperne *Calanus finmarchicus* og *C. hyperboreus*. Den første af disse to arter er næsten en indkomstgyder, der udelukkende er afhængig af den indkommende føde, hvoraf den anden er en kapitalgyder, der gemmer reserver for at gyde på et tidspunkt der er uafhængigt af fødetilgængelighed. Selvom de to arter er fra samme slægt, er deres størrelse ved gydemodenhed, og deres udbredelse meget forskellige. Vi undersøger effekten af deres ressource-allokeringstræk til reproduktion, koblet med den optimale størrelse ved gydemodenhed, som en funktion af længden på fødesæsonen (kapitel 5). I disse undersøgelser inkluderer vi adfærd og energetisk allokation. Kapitalgydning begunstiger stor størrelse ved gydemodenhed, og er succesfuld i korte opblomstringer, mens indkomstgydning er begunstiget i lange opblomstringer, og drager nytte af at være små. Da de resulterende fitnesskurvefunktioner ser forholdsvis ordinære ud, simplificerer vi modellen til en analytisk tilgang, som vi bruger til at undersøge det samme problem, og opnår tilsvarende resultater. Vi bruger herefter de lukkede udtryk til at undersøge parameterrummet, og de resulterende mønstre viser sig at være robuste (kapitel 6).

Denne afhandling fokuserer derfor på to primære aspekter af vandloppers livshistorie: daglig vertikal migration og reproduktiv strategi. Resultaterne kan generaliseres, og blive tilpasset til de fleste dyreplankton arter, der lever i et sæsonpræget miljø.

Preface

This thesis was submitted as part of the requirements to fulfill the Doctor of Philosophy Degree (PhD) at the Technical university of Denmark (DTU). The research presented was conducted between December 2010 and February 2014 at the National Institute of Denmark, part of the Technical University of Denmark (DTU Aqua) in Charlottenlund, and was financed by The Greenland Climate Research Centre, the Centre for Ocean Life (a VKR center of excellence supported by the Villum foundation) and by the Technical University of Denmark. The PhD was conducted under the supervision of Andre W. Visser and Ken H. Andersen, and included a one-month research visit to Bergen under the supervision of Øyvind Fiksen at the Biology Institute of the University of Bergen, Norway, in March 2013. A visit to Tromsø and Svalbard Universities were also undertaken under the supervision of Øystein Varpe in September 2012.

The graphics used for the first page, and to introduce each chapter, were created using the open source software Inkscape. Many thanks to the authors of this software and the community for the numerous tutorials and help available freely online. I would also like to thank Jan for the discussions on the illustrations. A 'lost' summer week was sufficient to follow enough introductory tutorials that revolutionized the oral and poster presentations of this work. The copepods in the front page were designed from a picture by Dag Altin and Ida B. Øverjordet, published in Berge et al. (2012). "The grasshopper and ant" parody illustration used in chapter 6 was inspired by the Grasshopper and the Ant fairytale from Jean de La Fontaine. "La cigale et la fourmie" is the first fairytale from the "Fable of La Fontaine" and describes a grasshopper enjoying the summer, but finding himself destituted when the winter starts. The antagonist is an ant who is working hard during the summer to store reserve, but survives comfortably during the winter. This story is a perfect analogy to the difference between income and capital breeding, a dichotomy in reproduction strategy explored in chapters 5 and 6. The income breeder spawns based on available food resource (i.e. the grasshopper sings during the abundant season), while the capital breeders store reserves as the ant does, in order to spawn detached from the feeding season. Thanks to Rodrigo Goncalves, who is the first one to have mentioned this possible example during a talk rehearsal in the lab.

Bibliography

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Aknowledgements

I am deeply grateful to my main supervisor, André W. Visser, for giving me the opportunity to pursue this highly fascinating PhD project and for his valuable support and interesting discussions throughout. He has been a great mentor over the past three years, and always reassured me with a welcoming smile. It has been a pleasure to get to know Andy, both in a professional and social setting, not least over a glass of wine at the famous Noma. I would also like to thank Ken H. Andersen, my co-supervisor, who first welcomed me to the institute for an internship during my Engineering studies in the summer of 2009, and allowed me to work with his former PhD student, Christina Frisk. Ken has been an important factor in my return to DTU Aqua for a PhD, and I greatly appreciate the opportunities and support he has given me during the years. I am also grateful to Uffe H. Thygesen for his help on the mathematical issues that I encountered during the PhD, especially the dynamic programming project. He has been an important actor in the successes of this project, and it has always been a privilege to collaborate with him.

A big thanks to Torkel G. Nielsen and his group for sharing their passion about the Arctic, in particular the *Calanus* copepods. Torkel also gave me the opportunity to participate in the PhD Course, "Fate of the Arctic spring bloom", that he organized at the research station in Disko Bay, West Greenland. Alongside, I would like to thank all the members of my working group during this PhD course: Clare, Peter, Miao, Øystein and Astthor for their enthusiasm in working on the diel vertical migration project and pursuing this adventure into a publication even though it is a bit far from most of our research fields. I would like to give a special acknowledgement to Astthor Gislason for bringing his Video Plankton Recorder all the way to Greenland and enabling us the opportunity to discover this amazing tool. Here I would also like to acknowledge Øystein Varpe, who has been an important player in my PhD project since I met him at this summer school. He has subsequently been a great help and support in different projects of my research. I also had the chance to discover his working places in Tromsø and Svalbard, which were incredible experiences that led to my crossing the Arctic circle! Øystein and I had the chance to meet with Mark Ohman at a meeting of the Centre for Ocean Life in Copenahgen, and I would like to

thank Mark for his push at a critical moment in the writing of the paper initiated in Greenland.

I am grateful for my current and former colleagues and friends: Jan, Christina, Lise, Fi, Sofia, Stavroula, Karin, Starrlight, Evandro, Rodrigo, Nis, Mie, Rasmus, Mette and Christian for their support and coffee breaks. They made these couple of years a pleasure, and the lab a second house to me. I would also like to thank all the member of the Center of Ocean Life, for the fascinating Wednesday meetings and modeling discussions. A special thanks to Nis for his help to translate the summuary and popular abstract to danish, and to Starrlight for her help on starting up this thesis' document settings in LaTeX.

I am immensely grateful to my family for their support in this 'adventure'. They have always been there for me, even with the distances, back in France for my parents and my sister, and ever further for my brother, his companion, and my young nephew. They have always been available and flexible with the timing of my research. An enormous thanks to my partner, Cameron, for his everyday support and discussion, for helping me organizing my thoughts and giving me advice. I know it has not been easy everyday, and I am not sure I would have been through without him.

Contents

Chapter 1

Synopsis and perspectives

Copepods dominate the zooplankton biomass in the world's oceans (Verity and Smetacek 1996), but how and why they do so remains an open question. They are adept swimmers, particularly suited to the visco-inertial hydrodynamics they inhabit. Their high clearance rate and their fast escape responses to predators have been suggested as the main factors of their success (Kiørboe 2011), although their reproductive behavior and ecology have also been invoked as giving them an advantage (Varpe 2012, Lampert 1989). Copepods of various species have successfully adapted to a wide variety of habitats; from the equator to the poles. Their broad geographical distribution, means that some species have had to adapt to living in strongly modulated seasonal environments. Specifically, in temperate to high latitude environment, they have to cope with annual cycles alternating between long harsh winters when little food is available, to a short but intense spring bloom when food is bountiful. The spring phytoplankton bloom that many copepod species rely on, is tightly linked to the local physical conditions (such as light, wind, currents) along with the amount of nutrients. For example, in high latitude ecosystems, the light regime changing quite abruptly from complete darkness to midnight sun, together with wind pattern and ice break-up, regulate the peak of phytoplankton bloom, and leave unproductive water the rest of the year. The annual cycle between harsh and bountiful conditions in these regions make it an ideal area to study how the behavior of copepods is adapted to maintain themselves as such successful members of the zooplankton community.

In addition to their evolutionary success, copepods are of particular interest in marine ecology as they are abundant and thus important link between the phytoplankton production and the upper levels of marine food webs. In particular they collect and store energy-rich lipids which are rich food source for higher trophic levels. They are therefore a significant interest in understanding the bottom-up limitation for the higher trophic levels including commercially exploited fish stocks (Varpe et al. 2005), as well as seabirds

(Karnovsky et al. 2003) and whales (Laidre et al. 2007, Falk-Petersen et al. 2009, Baumgartner et al. 2013).

The most striking behavior, adopted by copepods in seasonal environment, is their seasonal vertical migration. They can descend to a depth of 800 to 1500 meters for overwintering (Falk-Petersen et al. 2009), ascending again the following spring to feed and reproduce. The depth at which they find refuge is linked to the amount of lipids they store (Visser and Jónasdóttir 1999), the more they have, the better their ability to survive the winter. At these depths, in complete darkness, they find a refuge from predation, and a suitable habitat within which to overwinter. In the absence of food, and without the need for vigilance against predation, they enter a diapause stage (close to a hibernation), and can thus reduce their metabolic cost, allowing these small creatures to survive long winters. Before the spring bloom starts, they come out of their diapause stage, and swim up to the surface layer. Although the entry into diapause can easily be explained by a depletion of food availability, good internal state (i.e. a full lipid store), or an increase in predation pressure, the cues for the termination of the diapause stage remain elusive. Since the hypothesis on environmental cues such as photo-period has been refuted (Johnson et al. 2008), an internal state of reserve (lipid) controls has been advanced as a promising hypothesis (Visser and Jónasdóttir 1999, Maps et al. 2010) but still lacks sufficient study and proof.

In addition to this seasonal refuge at depth, copepods perform daily migrations between the food rich surface layer at night-time to safer deeper water during the day to escape the attentions of visual predators (Titelman and Fiksen 2004, Fiksen and Carlotti 1998). Daily migration has trade-off consequences for the success of individuals as it reduces their feeding opportunities (diminishing growth), but it is likely to increase survivorship, due to a reduced exposure to predation risk. This diel vertical migration (DVM) has been shown to be a very plastic response to seasonal changes in day-length, the light penetration depth, the presence of visual predators (such as fish or seals), of tactile predators (such as other copepods, chaetognath or ctenophore, Ohman 1990, Frost and Bollens 1992) and to the amount of food present at the surface (Fiksen and Carlotti 1998). For example, if their most abundant predators are fish, copepods are often found to perform DVM, but in presence of tactile predators which are themselves predated by fish, the copepods have been seen to change their pattern to a reverse migration (feeding up during the day, and finding refuge down at night, Ohman 1990, Frost and Bollens 1992). However, it is still unclear how DVM emerges and why there is so much variability between similar individuals, what the consequences are of this behavior in their life history, and how to include this behavior in models. These questions are addressed in 3 of the papers comprising this thesis (part I, and introduced in section 1.2).

In the high latitudes of the northern hemisphere, three species of the genus *Calanus* have notably succeeded in their adaptation: *Calanus finmarchicus* dominates the North Atlantic, *Calanus hyperboreus* the Arctic, and *Calanus glacialis* the Arctic shelves, the Barents Sea and the fjords (Conover 1988). These three species are particularly interesting, as they have developed remarkably complex life-histories which allow them to adapt to the harsh, seasonally modulated environment. Coming from the same genus, these three species are very closely related genetically, and undergo similar development pattern. They go through multiple moulting and shape changes in their life history: 6 stages of nauplii, with the first two being non-feeding stages and developing under internal storage given at birth, followed by 6 stages of copepodites, the last one being the adults able to spawn eggs (figure 1.1).

The copepodite torpedo shape is particularly efficient for swimming in viscous water, which is the way they perceive their environment due to their small sizes (Yen and Strickler 1996). They also perform similar migration behavior, undergoing seasonal and diel migration as mentioned previously.

The most striking difference between these three *Calanus* copepods is their difference of size (figure 1.2): *C. hyperboreus* for example can store up to 25 time more lipid reserves than *C. finmarchicus* (Falk-Petersen et al. 2007). Thus, *C. finmarchicus* is ranging between 1.9 to 3.2 mm in prosome length, *C. glacialis* up to 4.4 mm, while *C. hyperboreus* can reach up to 7.4 mm in prosome length (e.g. Frost 1974, Hirche 1997, Madsen et al. 2001). Size at maturity is of great importance in terms of life history strategies as it affects the time needed to reach maturity size, their storage capacity but also their predation mortality. In the marine ecosystems, we assume that the predation rate decreases with size [1] (Peterson and Wroblewski 1984, Hirst and Kiørboe 2002, Brown et al. 2004, Andersen and Beyer 2006). However, the case of the copepods is more complex as they change their vulnerability to different types of predation. Indeed, while they are small, particularly in the nauplii stage, they are very vulnerable to the abundant tactile predators such as chaetognaths, jelly plankton (e.g. ctenophores) as well as other copepods. However at larger size, they outgrow the preferred prey size range of most of these predators, but are more easily seen by visual predators such as fish (Huse and Fiksen 2010), and seabirds (Karnovsky et al. 2003)[2]. Thus, smaller maturity size, short life span, and high fecundity are often found in high predation, high abundance environments, while the longer life species are found in more extreme environments but with a reduced predation mortality (Stearns and Koella 1986). It is the case for *C. hyperboreus* found in

[1] A common allometric scaling for predation mortality rate p that I will follow is $p \sim w^{-1/4}$ where w is the weight of an individual.

[2] In high concentrations, they also become targeted by baleen whales (e.g. right, fin and sei whales); Nemoto et al. (1970)

the center of the Arctic Ocean where the level of predators are believed to be lower than in the fjords and the Arctic continental shelves, where the smaller *C. glacialis* seems to perform better (Berge et al. 2012).

Along with the different maturity sizes, their reproduction strategies also differ. Specifically, how and when resources are allocated to immediate reproduction, or to storage for future reproduction vary markedly between these closely related species. The small *C. finmarchicus* is fairly close to a pure income breeder, allocating directly their resource to reproduction once they are adults. Thus, their spawning period is tightly controlled by the timing of the spring phytoplankton bloom. At the other end of the spectrum, the large *C. hyperboreus* spawns in the deep during the winter,

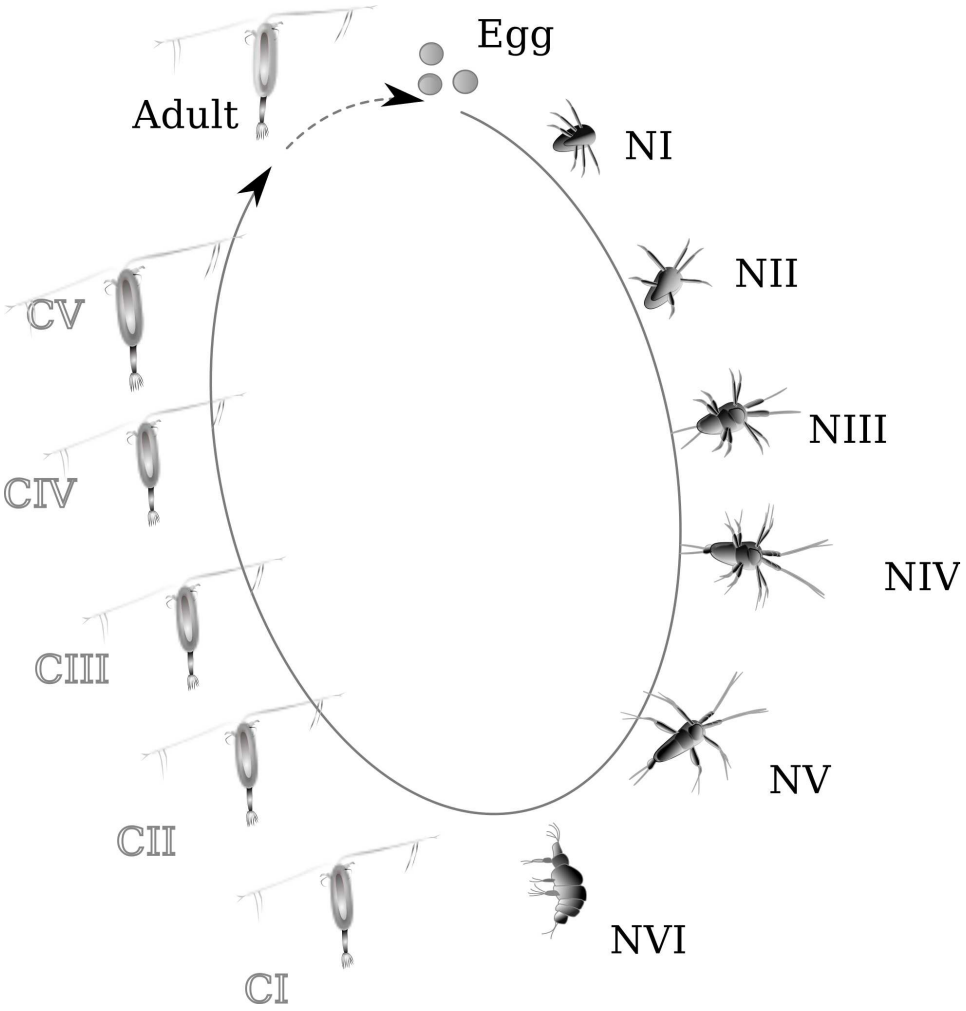

Figure 1.1: Development stages of copepods: from eggs to 6 stages of nauplii (NI to NVI), followed by 6 stages of copepodites (CI to CV plus the adult stage).

where there is a complete absence of food and relying on their internal storage. Thus, *C. hyperboreus* has to store a large amount of reserves to be able to spawn detached from the spring bloom. This strategy seems risky since individuals take the risk of dying before having a chance to spread their genes. However, it has the main advantage that the spawning can occur at a time suitable for the copepod offspring. Thus, capital breeders favor fewer offspring with a better chance of survival than a large number with a low fitness. In the case of copepods, the best time to be born is prior to the spring bloom (Varpe et al. 2007), allowing the offspring time to develop in their first nauplii stages in the absence of food, and being able to enjoy the full duration of the spring bloom. Between these two extremes, *C. glacialis* adopts a mixed strategy, spawning prior to the bloom based on their internal reserves, and doing some income breeding during the bloom. This species is particularly successful in the shelves and fjords which offer two bloom peaks per year, one with the sea-ice algal growth and one in the open ocean (Søreide et al. 2010). In these circumstances one can ask, what is the best reproduction strategy as a function of the environmental

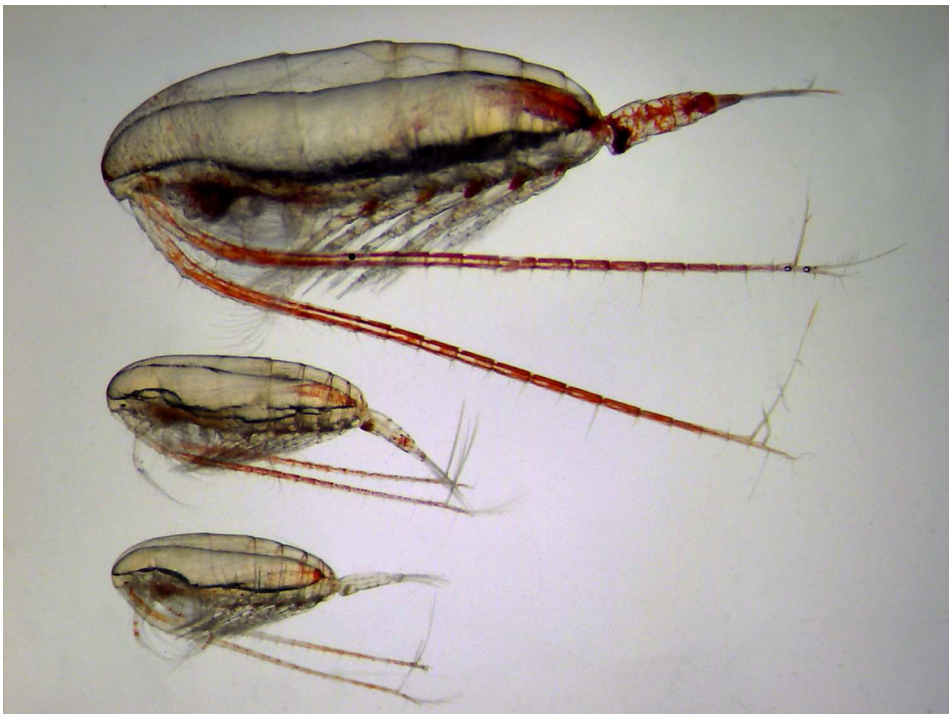

Figure 1.2: Arctic *Calanus* species. From top to bottom: females of *C. hyperboreus*, *C. glacialis* and *C. finmarchicus*. From net-haul in Kongsfjorden, Spitzbergen. Photo: Ida Beathe Øverjordet and Dag Altin. Front cover of the Journal of Plankton Research, March 2012, 34(3). Reprinted with permissions.

conditions? Is it better to be large or small? Is it better to be an income or a capital breeder? These questions are addressed in 2 papers of this thesis (part II, and introduced in section 1.3).

1.1 Modelling the environment

The circumstances in which diel vertical migration behavior and reproduction traits (timing and size at maturity) can be hypothesized to be tightly linked to environmental conditions in nature. Variation in these environmental conditions are thus explored to study the emergence of dominant strategies. Due to their small size and the fact that they feed on the low end of the primary production, copepods face harsh environments in temperate and high latitude ecosystems, where the strong seasonality of light, temperature and wind mixing leave them without food for months. Leaving temperature aside, latitudinal gradients are modeled as a variation of the yearly cycle of daylight hours per day. Indeed the sum of daylight hours per year is constant through the globe, but the repartition through the year differs greatly with latitude (figure 1.3 a), due to its dependence with the sun-earth angle [3]. In this thesis a useful model developed by Forsythe et al. (1995) is used to compute the number of hours of daylight for a given time of the year and latitude. The light intensity is used in chapter 4 as an indicator of the predation mortality at a given depth. Surface light intensity, for a given time of the year and latitude, is modeled based on the equation developed by Brock (1981) and is one of the main factors influencing the light penetration depth in the water column (light is assumed to follow an exponential decay with depth), i.e. the depth at which a copepod has to swim to in order to find refuge from visual predation during day-time.

Even though the spring bloom duration and timing are related to the latitudinal gradient, the phytoplankton bloom is also strongly influenced by local conditions (e.g. winds, depth, amount of nutrients in the system, sea ice breakup). However in the open ocean, one can clearly observe a delay in the production with increasing latitude, with a general trend of shorter but more intense blooms further north (e.g. Leu et al. 2011). In most of the papers of this thesis, I use a fairly simple model of the annual cycle of food availability. Namely, in any given setting, food availability is determined by two basic parameters; the timing (e.g. when the maximum occurs) and the duration of the bloom. In addition, to avoid confounding effects of a systematic variation in net production, it is assumed that the total annual food availability is constant. Thus, the effect of the spring bloom duration on behavioral strategy can be investigated, by modeling the

[3] More properly, the offset of the earths equational plane, and the plane of the elliptic, which is currently about 23.4^o, sets amongst other things, the polar circle and the tropic of cancer.

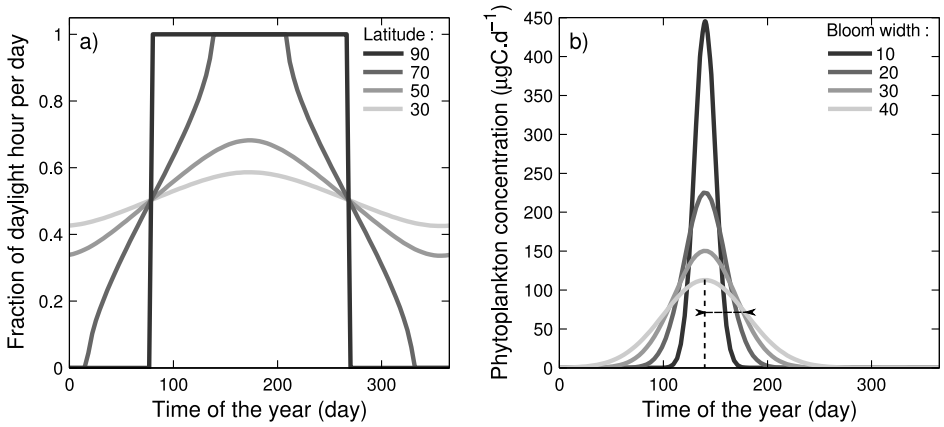

Figure 1.3: Fraction of daylight hour per day for different latitudes through a year (a, modeled by Forsythe et al. 1995), and variation of the food peak level when varying the width of the bloom (express in days), and keeping the amount of nutrient constant in the system (b).

bloom with a Gaussian function (figure 1.3 b). This assumption implies that when looking at the duration of the bloom, the maximum level of the phytoplankton bloom varies inversely: short blooms imply high peaks of food concentration; long blooms imply small. For the copepods, the level of food affects them as soon they are no longer saturated (no longer enough food as they can handle). Under saturation implies a longer time spent at the surface when considering the daily migration (and thus a higher exposure to predation mortality) and/or a slower growth (effect clearly seen in chapter 4).

1.2 Diel vertical migration: observation, emergence and implications

Diel vertical migration (DVM) consists of an ascent to the surface to feed on the phytoplankton layer at night, and a descent at dawn into safer layers. It has been shown as a response of zooplankton against the presence of visual hunters (e.g. fish), since they are the most efficient in the presence of light (e.g. Lampert 1989), when the abundance of food at the surface is sufficient to maintain growth. It seems to be an adaptable response to the type and abundance of predators (e.g. Ohman 1990, Frost and Bollens 1992) but also to the food concentration at the surface (Fiksen and Giske 1995). DVM is thus a trade-off between growth, investment in reproduction and predation risk which varies over the life time of individuals and over environmental conditions.

Even through DVM is relatively well studied, its understanding and im-

plications are still not fully understood (Pearre 2003). Three chapters of this thesis treat different aspects of the problem from observations (cf. section 1.2.1 - chapter 2), emergence (cf. section 1.2.2 - chapter 3) and implications (cf. section 1.2.3 - chapter 4).

1.2.1 A Video recorder study

An effective way to study diel vertical migration is to use a video plankton recorder (VPR). This camera can be submerged down through the column of water and take pictures at a speed of 15 per second (see pictures of the VPR in figure 1.4). Individual taxa can then be identified in the picture (e.g. figure 2.2) and, with an on-board CTD, be linked to the environmental conditions (such as depth, salinity, temperature, light or even fluorescence, a proxy for the concentration of phytoplankton). One such camera was used during the PhD course (titled "Fate of the Arctic Spring Bloom", sponsored by Nordforsk) taken during the spring of 2012 in Disko Bay, Western Greenland (see map in figure 1.5). This course was held during the phytoplankton bloom, which allowed for a study of the daily migration pattern of zooplankton. Four field of view settings were available on the VPR, but we used the 24 mm x 24 mm configuration in order to target copepod observation. The

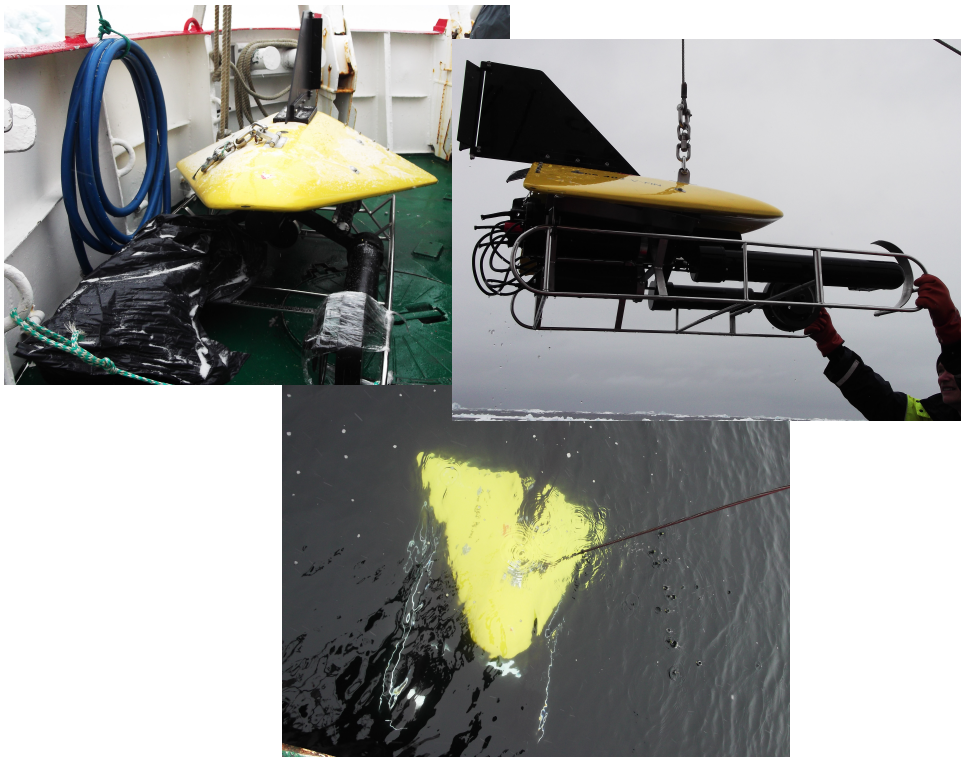

Figure 1.4: Pictures of the VPR used for the study in Disko Bay

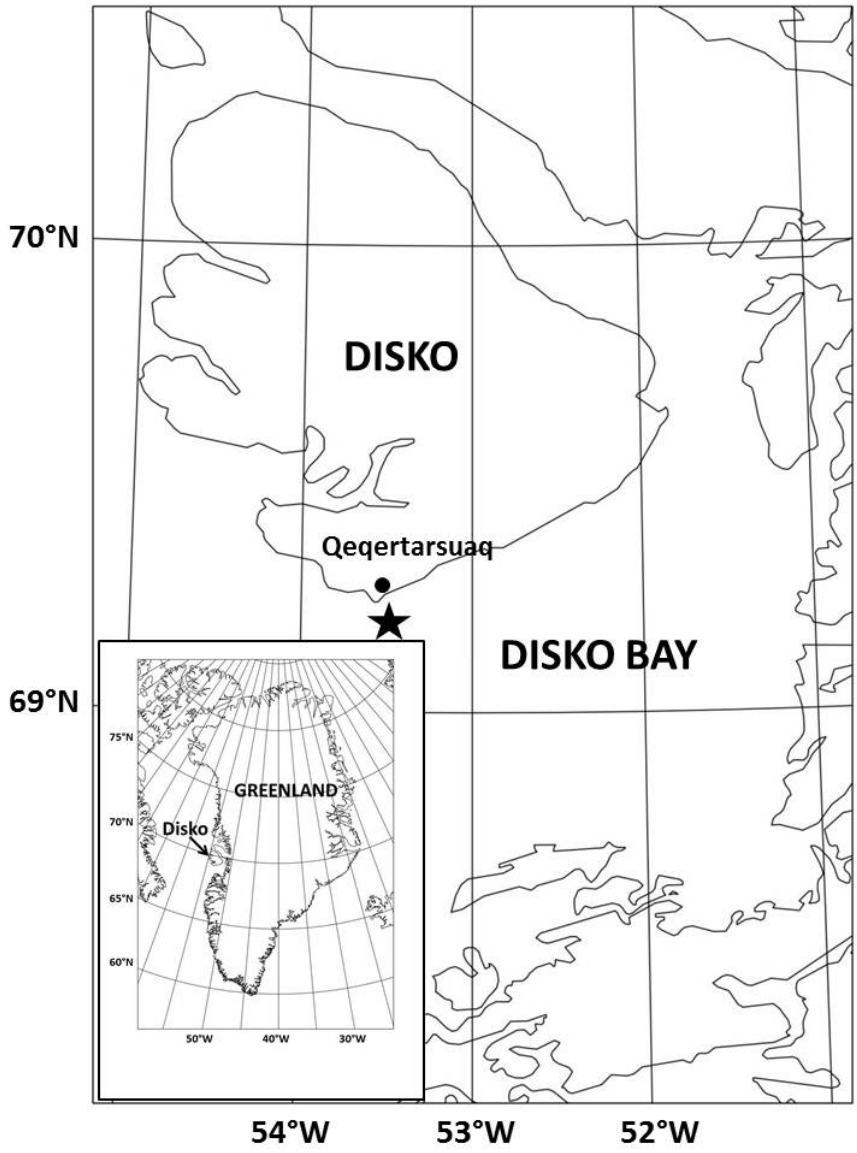

Figure 1.5: Map of Disko Bay, western Greenland (author: Miao Wang).

migration pattern of krill and ostracods could also be monitored. These three taxa perform very diverse migration patterns, from a very clear diel vertical migration for krill, a diel vertical migration but with quite a lot of variance in the copepod case, and a permanent deep habitat with the ostracods (figure 2.4). Other taxas were also observed, including amphipods, *pseudocalanus*, ctenophore and chaetognath, but their low sampling size did not allow further analysis. However their presence in the sampling effort was a good indication of the zooplankton community and of the presence of copepod tactile predators.

The main advantage of a VPR method is the precise position in the column obtained, in contrast with more common methods such as net sampling which integrates over the entire capture range (often over 50 meters, Pinel-Alloul 1995, Pearre 2003). It also has the advantage of allowing the possibility to distinguish between different species that the acoustic sampling cannot perform (e.g. Berge et al. 2009). As the quality of the pictures are of high resolution/quality (e.g. figure 2.2), informations regarding the state of the individual can also be extracted, such as their size or the presence of oil sac. It is also possible to see if individuals are carrying eggs, which may otherwise be lost in the nets (Corkett and McLaren 1979). In this study (chapter 2), the focus was chosen on the surface depth avoidance of copepods and on the effect of *Calanus* spp. size on their depth distribution between day and night during a 24h study. The depth below which 75% of the copepods were found was 45 meters during the night, while they were found deeper at around 91 meters during the days (figure 2.6). The light intensity at the surface seems also to have an effect on the day distribution, but unfortunately a technical issue during the first day's sampling prevented a complete analysis on this topic. According to their day and night positions, copepods seem to be present at a constant light intensity level (figure 2.7), suggesting that they follow an isolume. The size of the *Calanus* spp. influenced their daily migration, with a clear DVM on small size, while the larger individuals opted for a constant deep habitat, or even a reverse DVM (figure 2.8).

A manuscript on this study has been prepared "*Inter and intra-specific diurnal habitat selection of zooplankton during the spring bloom*" together with co-authors Astthor Gislason, Jan Heuschele, Clare Webster, Peter Sylvander, Miao Wang and Øystein Varpe, following a PhD course during which the sampling was made. This manuscript has been submitted to the journal of *Marine Biology* (cf. Chapter 2).

1.2.2 A game theory approach

Planktivors have their main source of food at the phytoplankton layer. Phytoplankton need light to grow, and thus their layer is in the light penetration

depth range (i.e. close to the surface). Even though some cells are sinking, most of the algae stays close to the surface (i.e. above the pycnocline). Planktivors therefore would prefer to spend time in this layer. Unfortunately for them, it is also where their own predators are the most efficient, since light helps their visual acuity. This interplay between planktivours (e.g. copepods) and their visual predators (e.g. fish) can therefore be seen as a predator-prey game.

Game theory has been developed in a goal to find the best strategy that one can adopt, whatever the competitor strategy is. A game theory approach was applied to the fish/copepod system (chapter 3), and the environment divided in two habitats: a surface habitat, affected by the daylight cycle but where copepod can find food; and a deep dark habitat, where copepods have very little food, but where the search efficient of fish are reduced (refuge habitat for the copepod). Both players have the choice to stay at the surface, stay in the deep, or perform diel vertical migration (in the surface habitat during the night, and in the deep habitat during the day; figure 1.6). Note that the migration strategy seems to be advantageous only for the prey (copepod), as the fish following this strategy will never get to enjoy their high visual acuity by staying in the dark. However, fish could have the advantage to follow its prey's migration pattern to match the distribution of their food supply. The asset of game theory is to include the response of the predator (and thus to have knowledge about them), which is generally rare in models focusing on plankton.

Three scenarios are explored: first, only the prey (copepods) have the possibility to choose the diel vertical migration strategy, while the predator (fish) can only stay in one of the habitats all day long; secondly both predator and prey can choose one of the three strategies, while the third scenario explores the influence of a top predator, present in the surface habitat and predating only on the middle predator (fish), thereby affecting the behavior of the middle predator and therefore of the prey behavior.

The first striking result is the emergence of the migration pattern as soon as the loss from predation balances the possible gain (growth rate) at the surface (figure 3.1 and 3.2). Predators match the distribution of their prey when they are all at the surface (in the case of low daylight predator voracity, and high potential growth for the prey). When the prey are migrating, predators divide themselves between the surface habitat and the deep (scenario 1, figure 3.1) or the migration strategy (scenario 2, figure 3.2), with a higher proportion at the surface when the surface growth rate of the prey is higher. Hence, part of the population stays at the surface, scaring the prey away from the productive habitat, while the other fraction of predators follow the prey's migration pattern. Note here that even though individuals within a population do not perform the same strategy, they have the same fitness. This emergence of a mixed strategy is one of the main

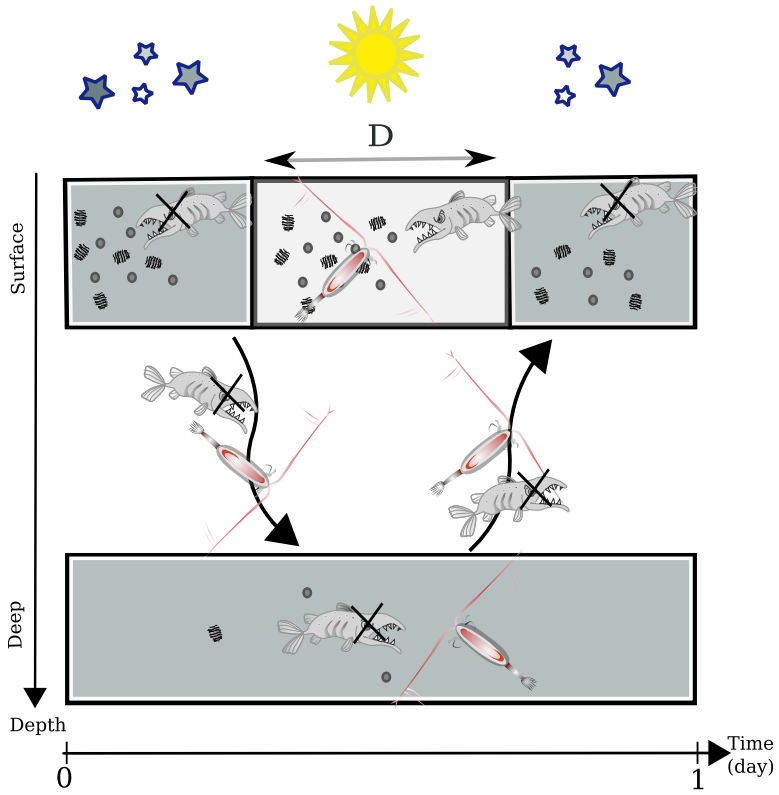

Figure 1.6: Game theory set-up: the environment is divided in 2 habitats: the surface habitat where copepods have food, but where the fish benefit from their high visual acuity during the day and; the deep habitat, a refuge for the prey as the darkness alter the performance of their visual predator, but where the food is scarce.

advantages of applying game theory, since it may account these different strategies, even without proper implementation of density dependence (as in our case). In the field, it is always a bit unclear why individuals apparently similar do not perform the same strategy and this can be one of the reasons.

When introducing a top predator in the surface habitat, foraging only on the middle predator, the behavior of both the prey and the middle predator are affected. The predator are now scared away from the surface habitat, providing an opportunity at the surface for the prey (figure 3.3). Hence the position, and composition of the food web, matters for the optimal behavior of individuals.

The paper "*Diel vertical migration arising in a habitat selection game*" was written in collaboration with Uffe H. Thygesen and André W. Visser, and was published in the journal of *Theoretical Ecology* (Sainmont et al. 2013; cf. Chapter 3).

1.2.3 A simple approach to include diel vertical migration in models

If game theory is a great tool to investigate the interaction between players, it is not always fit for full life-history models. Indeed, the diel vertical migration strategy set-up used in chapter 3 is not robust to midnight sun (the migration strategy ends up being the same as the deep habitat strategy), and information about visual predators are not often available or implemented in detail when studying the zooplankton level. Behavioral optimization over the complete life of an individual, and over seasonal cycles, requires techniques such as dynamic programming or genetic algorithm, which takes into account the current and future individual's state and the environmental conditions in the optimal solution.

The disadvantages of methods like dynamic programming and genetic algorithm are their high computational demands, their complexity to set up and their framework rigidity (Bellman 1957). They are thus often unsuited to include in large models. As an alternative, myopic methods based only on the current individual state and environmental conditions have shown promising results in conservation biology. In chapter 4, myopic methods of diel vertical migration with the "optimal" solution given by dynamic programming are compared. The environmental set-up is fairly similar to the one used with the game theory study (figure 1.6), except it is assumed that no food is available in the deep habitats (figure 1.7). Leaving aside the visual predator behavior, zooplankton (copepod like individuals) are focused on, and it is assumed that they come to feed at the surface at least during the night-time during the bloom. In complete absence of food at the surface, it is assumed that they enter a diapause stage, hence reducing their metabolic cost, and predation mortality thanks to a refuge habitat.

The question remains, how much time of the day do individuals want to spend at the surface feeding instead of finding refuge in the deep habitat? Note that the myopic method is equivalent to the dynamic programming and generic algorithms when the environment is fixed (aseasonal, figure 4.F.1), i.e. a constant environment where there is no advantage to know the future (or more exactly, it is already known to be the same as today's). The differences between the dynamic programming method and the myopic approximation in seasonal environment are investigated by comparing individual's life-time expected reproduction output (how many eggs is an individual expected to produce during its life time, adjusted by its probability to be alive at the spawning time) following each strategy. Their disparity over different latitude, bloom duration (as in figure 1.3 b), background and predation mortality are investigated. Predation mortality is affected by the abundance of fish, the amount of daylight hour per day (figure 1.3 a) and the light intensity at the surface and in the refuge habitat.

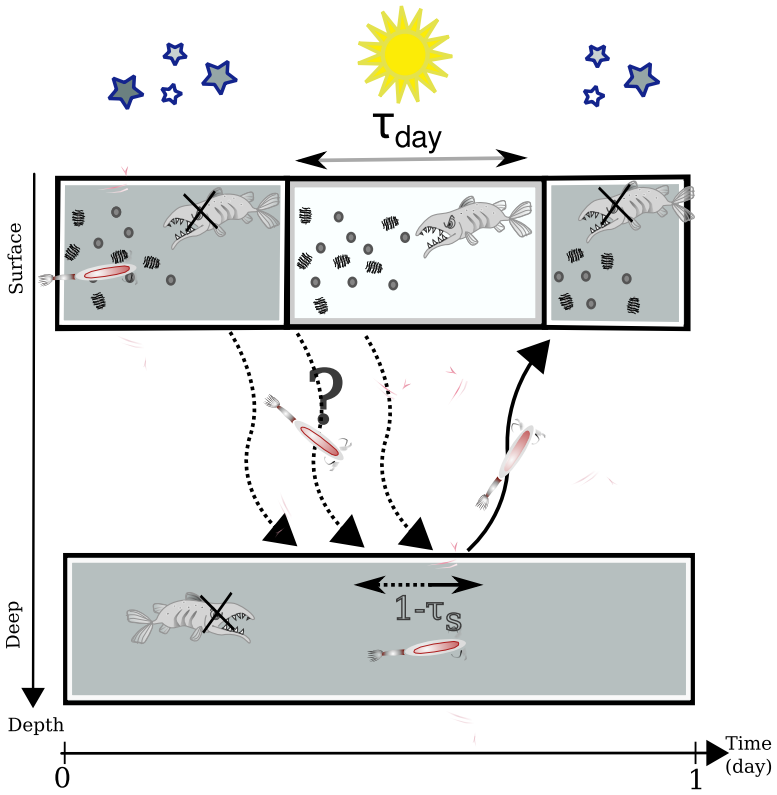

Figure 1.7: Model set-up: the environment is divided into 2 habitats: the surface habitat where copepods have food, but where the fish benefit from their high visual acuity during the day and; the deep habitat, a refuge for the prey as the darkness alter the performance of their visual predator, but where the food is absent. The question is when do the copepods want to find refuge in the deep during day-time? Or, how much time of the day do individuals want to spend at the surface feeding under high predation mortality. Note here that the depth of the refuge habitat varies with the individual capacity to swim (link to individual size), and that the predation mortality rate is also a function of the size of the copepods, of the light intensity, and the abundance of fish.

Note how well an individual following the myopic approximation method is doing compared to an individual staying at the surface (null strategy; cf. figure 4.4). Thus, any kind of optimization behavior of diel vertical migration is better than none. The second result is that the myopic approximation gives rather decent results when compared to the dynamic programming prediction, especially with a low or moderate predation mortality (figure 4.3), and when the environmental conditions are not too harsh (decrease of performance in short blooms and high latitudes, figure 4.2).

It is thus argued that a myopic method can be used to model diel vertical

migration in large models, when methods such as dynamic programming or genetic algorithms are not an option due to their computational demands. For example, it can be particularly useful in a bio-geographic model, where the zooplankton diel vertical migration affects the carbon flux in the ocean.

The manuscript "*Myopic heuristics versus life-time optimization of daily routines in seasonal environments*" has been prepared in collaboration with Ken H. Andersen, Uffe H. Thygesen, Øyvind Fiksen and André W. Visser, and is going to be submitted shortly to the journal *Oikos* (cf. Chapter 4).

1.3 Resource allocation to reproduction: income versus capital breeding

Resource allocation to reproduction shape the offspring's abundance but also their chances of survival. Similarly to the r- (small resource allocation per egg; i.e. many small offspring) and the K- (few large offspring) strategies, the trade-off between direct allocation of incoming resources to egg fueling (income breeding strategy) and delayed allocation depending on reserve storage, frame the success of a species in a given environment. Indeed, the timing of reproduction compared to the feeding season impacts the chances that offspring reach the needed size to overwinter - the main bottleneck that individuals are facing in harsh seasonal environments.

1.3.1 An individual based model study

An individual based model (IBM) is used to approach the question of the best reproduction strategy and the best size at maturity. Behavior is included alongside a system of resource allocation to cover metabolic cost, somatic growth and reserves, together with an implicit influence of offspring time of birth on population growth. Individual behavior combines a deterministic timing of overwintering linked to the feeding season periods, and a myopic approach to diel vertical migration, influencing feeding rate and predation mortality.

As presented in the drawing introducing chapter 5, the food intake covers first of all the metabolic cost, while the surplus is allocated to the somatic growth until the maturity size is reached and then to the reserves pool. Daylight variation over the year and food availability are modeled as introduced earlier in section 1.1 - figure 1.3 a & b. Diel vertical migration behavior is optimized with a myopic method similar to the one presented in chapter 4, but slightly more simplistic (cf. Appendix 5.A). The difference mainly resides in the fact that the deep habitat depth is fixed (not as a function of individual size) and that the gain in predation mortality in this refuge is a constant fraction of the predation mortality at the surface. Ultimately, the

same myopic methods as outlined in chapter 4 will be implemented.

We test our two pure reproduction strategies as a function of the duration of the feeding season for a given latitude by following cohorts (also called super-individuals) set by date of birth. Indeed, individuals born in the same date are assumed to be identical as they experience the same environmental conditions in this deterministic growth model. Note that we assume capital breeders to always spawn at the same time of the year, hence only one cohort per year is needed for this strategy. On the other hand, income breeders spawn continuously during the feeding season, by using the extra food resource to fuel egg production as soon as they are mature and, thus multiple cohorts per year are needed to describe this reproduction trait. We allow for multi-year development. Since there is no density-dependence, the population growth rate is used to compare the strategies (combination of size at birth and reproduction trait) and determine their success in various environments (feeding season duration and latitude).

The model is first used to find what is the best spawning time for capital breeders. By spawning prior to the bloom, parents would optimize their offspring chances of survival (Varpe et al. 2007), since they would benefit from the full duration of the feeding season. However, the parents would suffer longer from mortality and would then take the risk of dying before contributing to the next generation. The model predicts that it is indeed the parents which are taking the most risk to give their offspring a larger chance of survival (figure 5.2). By using the best spawning time for capital breeders, the model concludes that it is better to be a large capital breeder when the feeding season is short, while it is advantageous to be as small an income breeder as possible when the feeding season is long (figure 5.3).

The work in the manuscript "*Income versus capital spawning at high latitudes: modelling copepod reproductive strategies*" was a collaboration with Ken H. Andersen, Øystein Varpe and André W. Visser (cf. Chapter 5). This manuscript has been put on hold to explore the validity of the myopic approximation to model the diel vertical migration behavior (chapter 4) and to investigate the income versus capital breeding strategy with another method (cf. section 1.3.2 and 6). This manuscript is intended to be modified to include the same DVM myopic methods as chapter 4, and to investigate the effect of this behavior optimization on the two reproduction strategies. The individual based model can then be used to address other ecological questions such as the effect of multi-year life cycle, of latitudinal gradient or inter-annual variation in food availability (cf. section 1.4 - Perspectives and outlook).

1.3.2 Capital versus income breeding: an analytical model

As the capital and income fitness curves as a function of the feeding season duration observed in figure 5.3 seem to be fairly standard (saturating function in the case of the capital breeders and an exponential growth for the income breeders), the same problem is investigated using an analytical model (Chapter 6). Mathematical models require great simplification of the setting to be resolvable but have the main advantages that they give a close solution which can then be used to explore (rapidly and easily) the parameter space - i.e. the fastest way to test the result pattern robustness.

The food availability modeled with a Gaussian function is therefore simplified to an on and off function, by assuming that when food is present, individuals are saturated and are thus feeding at their maximum consumption rate. The DVM behavior and the daylight cycle through the year are also ignored. Overwintering is taken into account by having a reduced metabolic cost and reduced predation mortality as soon as there is no food available, simulating the retreat to overwintering at depth. The separation between somatic and reserves is not explicit any longer, and a one-year cycle only is considered.

Writing the equation also requires the identification of bottlenecks in the population yearly cycle. For the capital breeders, it is the spawning at a given time of the year. Assuming that this date is fixed and a heritable trait, an egg born at time t_0 is considered and the number of eggs produced by this standardized individual a year later (time t_0+1, figure 6.1 A) is investigated. On the other hand, the main environmental pressure for income breeders is to reach a suitable size before the winter begins. We thus start with an adult at the beginning of the winter and count the number of mature individual at the end of the next feeding season. Note that the equation for this strategy is a bit more complex than for the capital breeders due to the possibility of multiple generations within the feeding season (figure 6.1 B) and can be resolved thanks to the assumption of constant food level (see equation 6.13 and appendix 6.A).

Similar result patterns were found with respect to the IBM method (chapter 5 - figure 5.3) with success alternating between large capital breeders in short feeding season and small income breeders in long productive seasons (figure 6.1). Indeed, capital breeders are quickly limited by their storage capacity in long feeding seasons, but this also pushes them to grow to a larger size to increase their reserve storage. On the other hand, small income breeders are notably successful in long blooms because they reach maturity size fast and can thus have several generations per year. This pattern is revealing strong robustness in all the parameters used in the model (figure 6.2).

The work in this paper "*Capital versus income breeding in seasonal environment*", in collaboration with my co-supervisor Ken H. Andersen, Øystein Varpe and my supervisor André W. Visser, was submitted to the journal of *American Naturalist* (cf. Chapter 6)[4].

1.4 Perspectives and outlook

Two important aspects of the copepod life-history are investigated in this thesis: a plastic behavior (Diel vertical migration - Part I) and an inherent/heritable trait (reproduction strategy - Part II). The success of these strategies depends on how the environmental conditions shape the success of individual traits through growth, mortality and breeding.

The two modeling approaches in the dichotomy between capital and income breeding (chapter 5 and 6) show that sometimes complex set-ups and life-history details do not always matter to find the right pattern. However, going through, sometimes tedious, modeling processes such as IBMs can broaden perspectives on the simplicity of the trait-based responses to environmental conditions. Analytical models have the drawback that they are quickly limited by the amount of details that can be added while still being able to find closed–form solutions. They are nevertheless the most suitable type of models to explore the robustness of results through the parameter space; exploration which can otherwise be time-consuming and computationally demanding with other modeling methods. IBMs, on the other hand, allow for the understanding of the effect of many behaviors and traits which can be easily be embedded. Thus, the model developed in chapter 5 can, for example, be used to test the effect of diel vertical migration on the two breeding strategies. One could also investigate the benefit of multi-year cycles, the repercussions of an increase of predation mortality toward the end of the feeding season and/or, the potential value in overwintering before the end of the feeding season. The IBM also offers the possibility to study the impact of variable environments (i.e. modification of the timing and/or duration of the feeding season inter-annually) on the breeding strategies.

As mentioned in the introduction, a third species (*Calanus glacialis*) is

[4]The illustration used for this chapter is inspired by the Jean de la Fontaine fable "the grasshopper and the ant" using copepod characters, where the grasshopper is described as enjoying the summer, relying on the food available at that time but does not have anything when the winter comes (as the income breeders relies on food availability to fuel their egg production but does not store reserve to survive the winter), while the ant works hard to store reserves during the summer but can rely on them to survive the winter (as the capital breeders store reserve to which allow them to survive the winter and spawn at a time that disconnected with the timing of the spring bloom, and is beneficial for their offspring)

co-existing with the *C. finmarchicus* and *C. hyperboreus*, for which their reproduction strategy and size at maturity are explained in chapter 5 and 6. The *C. glacialis* reproduction strategy is situated in the trait spectrum between income and capital breeding, and as a slightly larger size than *C. finmarchicus* but still far smaller than *C. hyperboreus* (cf. figure 1.2). By playing with the cost and benefit of both breeding strategies, mixed strategies is in some circumstances beneficial and a good compromise in the trade-off of resource allocation to reproduction and maturity size. For example, *C. glacialis* combine the best of both world, being able to spawn early in the season based on their reserves, and continue spawning during the spring bloom. They are quite successful in the fjords and the continental shelves where the feeding season occurs in two busts (Søreide et al. 2010). However, they seems quite sensitive to changes in the time lags between these two blooms.

Although this thesis was based on copepods, the life-history strategies studied are quite generals and some results can thus be extended to others organisms. Diel vertical migration is, for example, a very common behavior among zooplankton (e.g. Pearre 2003), and can also be seems in fish larvae, influencing the behavior of their predators (such as larger fish, e.g. tuna Dagorn et al. 2000; or penguins e.g. Bost et al. 2002). In a more general sense, daily cycles in habitat choice and trade-offs between foraging and predation risk, are processes that shape the behavioural ecology of many terrestrial animals as well. Income versus capital breeding have a long history of publications as this dichotomy is observed in many levels of the animal kingdom, as far as they are able to carry reserves.

In a context of climate change, studies about the species trait resilience give an indication as to the ability of populations to maintain themselves in a changing environment. While income breeders have a strong ability to propagate in long feeding season environment thanks to their fast population growth, their capacity to maintain themselves in a "bad" year is less clear. Thus, a warmer climate should benefit them but they will be less resilient to unpredictable weather pattern expected alongside climate change. Capital breeding, on the other hand, seems to be a robust strategy at the conditions that they do not miss the feeding season. On the other hand, they could well be out-competed by smaller income breeders if the weather become more clement. Variation in the copepod abundance and community composition would have a bottom up effect on larger species such as fish, sea birds or whales. Thus, within populations trade-offs in behavior and life-history strategy provide valuable insights into the species capacity to cope with environmental changes. Assessing the fate of these populations under the threat of climate change is a knowledge needed to help mitigate and manage local ecosystems.

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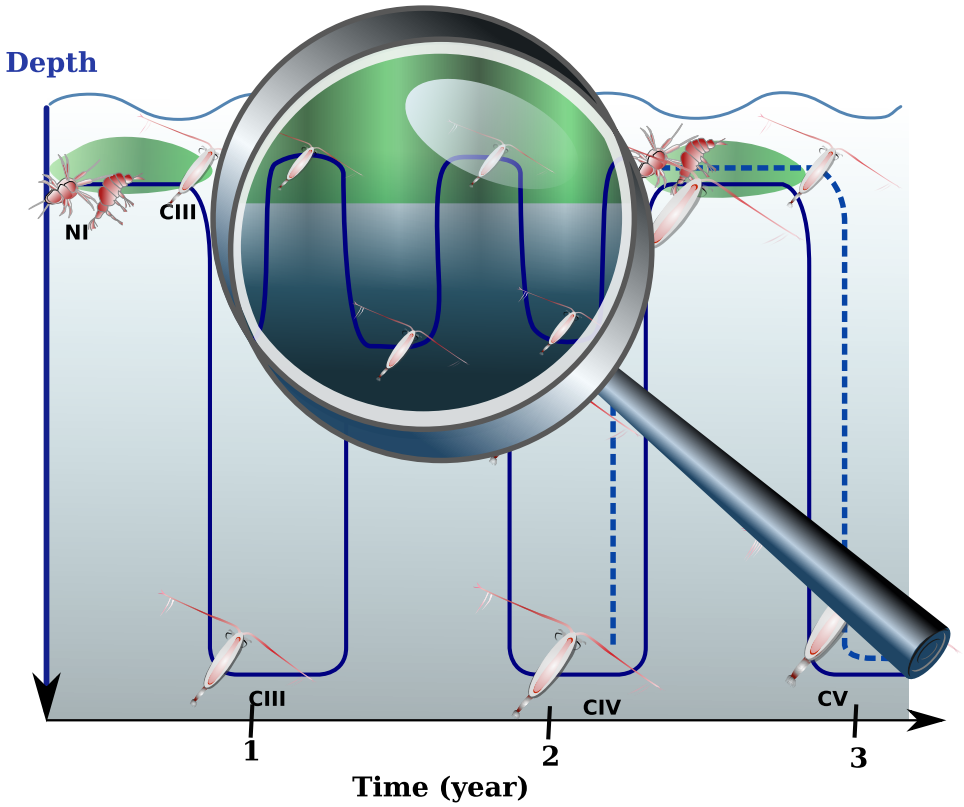
Part I

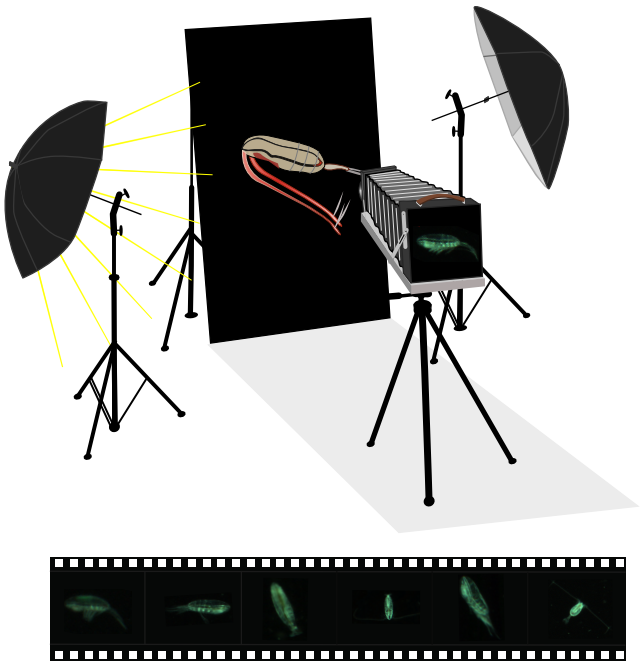
Diel vertical migration: observation, emergence and implications


Depth
NI
CIII
CIII
CIV
CV
1
2
3
Time (year)

Chapter 2

Inter and intra-specific diurnal habitat selection of zooplankton during the spring bloom

Sainmont, J., Gislason, A., Heuschele, J., Webster, C., Sylvander, P., Wang, M., and Varpe, Ø. (Submitted). *Marine Biology*



Inter and intra-specific diurnal habitat selection of zooplankton during the spring bloom observed by video plankton recorder

Abstract

Diel vertical migration (DVM) is a behavior adopted by most species of zooplankton at some point in their life cycle. DVM is an adaptation to avoid visual predation during daylight hours while still being able to feed on surface phytoplankton blooms during the night. Here we report on a DVM study using a video plankton recorder (VPR), a tool that allows mapping of vertical zooplankton distributions with a much greater spatial resolution than conventional zooplankton nets. The study took place over a full day-night cycle in Disko Bay, Greenland during the peak of the phytoplankton spring bloom. The sampling revealed a large abundance of copepods performing DVM (up during night and down during day-time) with strong intra- and inter-specific variability. Migration behavior was expressed differently among the abundant groups with either a strong DVM (euphausiids), a permanent deep habitat (ostracods) or a marked DVM signal driven by strong surface avoidance during the day but less clear depth preferences at night (*Calanus* spp.). The observed escape from surface waters during daytime reduces feeding opportunities but also lowers the risk of predation, and thereby is likely to influence both state and survival. *Calanus* spp. displayed state-dependent behavior, with DVM most apparent for smaller individuals, as well as an overall deeper residence depth for the larger individuals.

Keywords: pelagic ecology, predator-prey interactions, video plankton recorder, diel vertical migration, *Calanus*

2.1 Introduction

Theory predicts that feeding activity is traded off against the risk of exposure to predators (e.g. McNamara 1987). Many herbivorous and omnivorous zooplankton respond to predators by performing diel vertical migrations (DVM), feeding in surface waters at night, when low light levels minimize their exposure to visual predators, and spending the daytime in deeper and safer waters (Hays 2003). The pelagic is a diverse community where complex interactions and trophic cascades can take place (Ohman 1990, Baumgartner et al. 2011). Furthermore, species will differ in their motivation to migrate, based on factors such as their feeding mode and risk of being detected by predators. Similarly, intra-specific variability in traits such as energy reserves, size or maturity status lead to state-dependent DVM (Hays et al. 2001) and consequent variability in the vertical distribution of individuals within a population.

Measuring the distribution of plankton in the pelagic is a challenging task. Vertical net tows are most frequently used. One disadvantage with this method is that individuals within depth intervals are pooled, weakening the precision of our knowledge of their position and thereby reducing the power when testing for differences in depth distributions between day and night (Pinel-Alloul 1995, Pearre 2003). Acoustic methods can solve the issue of pooling over depth intervals, but they suffer from uncertainties regarding which species that are observed (e.g. Berge et al. 2009). Video and photographic techniques are alternatives to these dominating approaches. Video plankton recorders (VPRs) have been developed over the last decades and give exact information regarding the depth of an individual as well as providing quantitative estimates of plankton abundance as a given volume of water is imaged by the camera, with however the downside of a smaller sampling volume than nets and acoustic methods (e.g. Davis et al. 2005). An additional benefit is that the instrument provides concurrent data on hydrography (temperature, salinity, density) and phytoplankton biomass (chlorophyll *a* fluorescence) from the same parcel of water as imaged by the VPR, thus providing finely resolved information of the distribution of zooplankton in relation to the environment. Previous studies have shown that VPR data and nets give comparable information on concentrations of abundant taxa such as copepods (Benfield et al. 1996, Tiselius 1998).

We report on a VPR study of the zooplankton community at the Arctic to sub-Arctic location of Disko Bay, Western Greenland, during the annual spring bloom, a time of year when there are marked differences in the light levels between day and night, and the food availability for grazers is high. Disko Bay offers an ideal testing ground for process studies and the pelagic ecology of the Disko Bay system is well studied (e.g. Nielsen and Hansen 1995, Madsen et al. 2001, Turner et al. 2001, Hansen et al. 2003, Webster et al. prep) due to its proximity to an onshore biological station. The main

aim of the study was to detect which parts of the plankton community performed DVM. We expected larger species, which tend to be more easily detected by visual predators, to migrate more than smaller species. We discuss the extent of DVM observed in relation to life cycle strategies of the different species and families, acknowledging that the motivation for predator avoidance and feeding may be state-dependent, varying with ontogenetic stages, maturity levels and reproductive strategies.

2.2 Materials and Methods

2.2.1 Sampling

The sampling was conducted from the RV *Porsild* in Disko Bay 69°15'N, 53°33'W on 28-29 April 2012. A map of the area is available in Nielsen and Hansen (1995). A digital autonomous VPR from Seascan Inc. with inbuilt SBE-49 CTD and Wetlabs ECO Puck fluorometer/turbidity sensor was used to study the DVM of zooplankton. The VPR was supplied with a camera (Uniq model UC-1830CL) with 1 megapixel resolution (1024 x 1024), 10 bit color depth and a frame rate of compressed images of ∼15 per second. The VPR was lowered slowly (∼0.5 m s^{-1}) from the surface and to near the sea floor (∼300 m depth). Samples were obtained on four occasions, two day-time samplings and two night-time samplings. Each sampling event had three down casts and three up casts, except the first night-time sampling when two down casts and two up casts were made (Table 2.1). Due to issues with a corrupted file, only data from the first down cast was available on Day 1. Sea water temperature, salinity, density, fluorescence, and light intensity were measured by the VPR's CTD and by a Seabird SBE25-01 CTD. The CTD casts were made just before Day 1, the second night and Day 2 samplings. The Seabird CTD was lowered to near the seafloor and then raised to the surface again.

Table 2.1: The video plankton recorder was deployed four times encompassing day and night-time sampling from R/V *Porsild* in Disko Bay, Western Greenland in April 2012

Station	Date	Local Time (-2 UTC)	Depth (m)
Day 1	28/04/2012	13:02-14:24	0-349
Night 1a	28/04/2012	23:03-00:01	0-343
Night 1b	29/04/2012	01:25-02:40	0-320
Day2	29/04/2012	13:00-14:17	0-300

2.2.2 Light conditions

Surface light intensity was recorded on an onshore biological station approximately 12 km from the sampling site, throughout the sampling period. The VPR casts were made near the high and low peaks of daily light variation (Fig. 2.1). Light intensities in the water column were measured by a CTD prior to each VPR deployment. The data were used to calculate the light attenuation coefficient by fitting an exponential decay function over the depth:

$$I(d) = I_0 \exp(-\alpha d), \tag{2.1}$$

where I(d) is the light intensity at depth d, I_0 the light intensity at the surface and α the attenuation coefficient. α was estimated using a nonlinear (weighted) least-squares fitting procedure. We then calculated the model fit (R^2) by correlating model prediction and observed values from Day 2. We used a coefficient of 4.39 to convert the light measurement from watts per square meter (W m^{-2}) to photon irradiance (μmol photon s^{-1} m^{-2}), corresponding to a light wavelength of 525 nm.

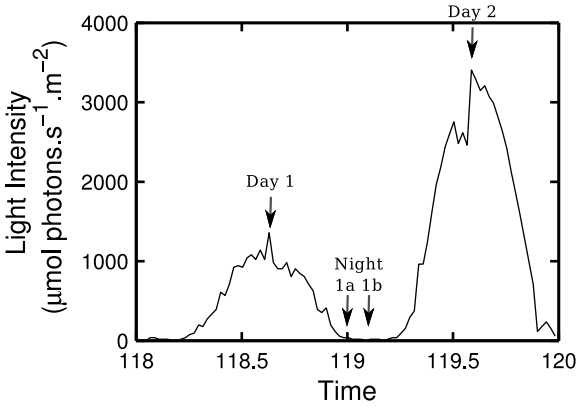


Figure 2.1: Surface light intensity throughout the study. Arrows indicate when the sampling took place

2.2.3 VPR specifications

Each VPR tow produces a file consisting of compressed images and the ancillary CTD and fluorescence data. The images were extracted as regions of interest (ROIs) employing a set of extraction parameters (e.g. segmentation threshold, and focus) using the software AutoDeck (Seascan Inc). The volume of seawater imaged by the VPR is the product of the field of view and the depth of field. When deploying the VPR, a setting with a field of view of 24 x 24 mm was used. The settings used in AutoDeck for extracting the images gave a depth of field of 32.3 mm and thus the imaged volume

was 18.6 ml (24 mm x 24 mm x 32.3 mm). The imaged volume and counts of manually sorted images were used to calculate abundances (individuals per m^{-3}). MATLAB was used to link the pictures to time and depth of observation.

2.2.4 Species identification and measurement

Sixteen taxa, genera or particle types were identified, and most of the copepods could be identified to genus (example of species photographed in the panel of Fig. 2.2). The identified categories were amphipods, euphausiids, copepods (with the subgroups of *Calanus* spp., *Metridia longa.*, *Pseudocalanus* spp. with eggs, *Paraeuchaeta* spp. with and without eggs, and unidentified), chaetognaths, cteno-phores, crustaceans, fecal pellets, irregular marine snow, jellyfish, ostracods, and others (Table 2.2). However, only the most abundant categories of animals were considered for our analyses (more than 25 detections over the four sampling events).

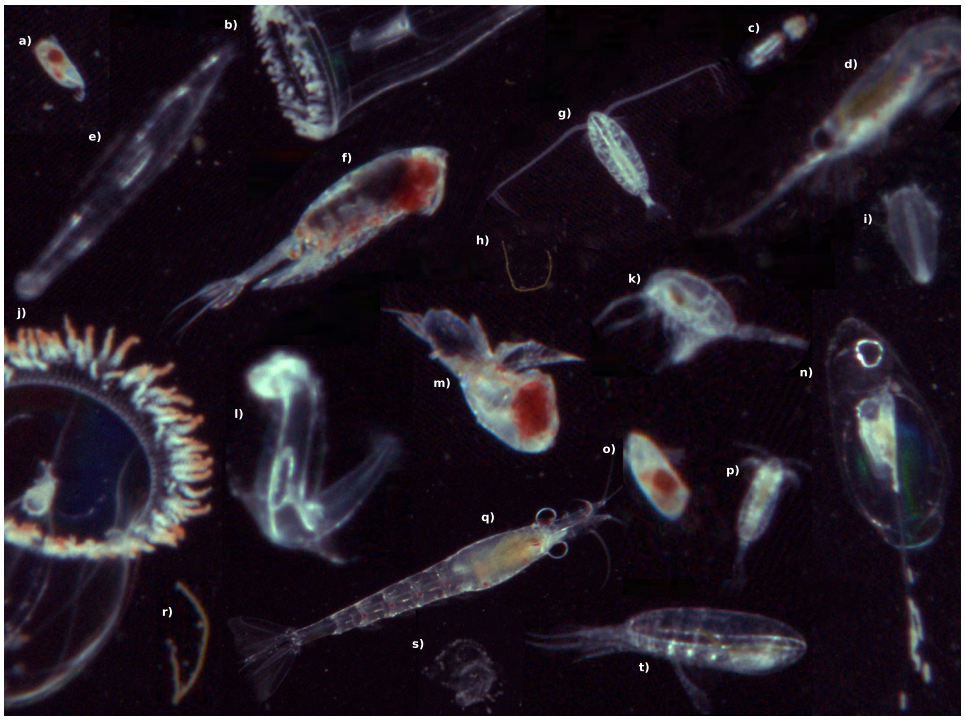


Figure 2.2: Selection of pictures taken by the VPR during our study. In the picture, there are ostracods (a, o), jellyfish (b, j, n), *Pseudocalanus* spp. with eggs (c), euphausiids (d, q), chaetognaths (e, l), *Paraeuchaeta* spp. without eggs (f, m), *Calanus* spp. (g, p, t), fecal pellets (h, r), *Metridia* spp. (k), ctenophore (i) and marine snow (s). Please note that the images are not to scale

Table 2.2: Abundance per squared meters of groups observed, averaged for all four deployments of the VPR. Standard deviation and range is also given

	Abundance (10^3 m^{-2})		
	mean	std	range
Fecal pellets	164.1	41.2	[74.1 - 251.3]
Copepods	62.4	25.5	[31.4 - 144.4]
Calanus spp.	46.5	19.3	[26.4 - 111.6]
Unidentified Copepods	10.5	7.8	[1.8 - 28.9]
Ostracods	5.3	3.5	[0.0 - 10.3]
Irregular marine snow	4.3	3.8	[0.0 - 15.1]
Others	4.0	2.2	[1.3 - 10.2]
Metridia	3.3	1.8	[1.3 - 6.8]
Euphausiids	2.4	1.9	[0.0 - 7.1]
Ctenophores	1.7	3.6	[0.0 - 13.9]
Jellyfish	1.7	1.7	[0.0 - 5.7]
Chaetognathas	1.3	1.4	[0.0 - 4.1]
Pseudocalanus with eggs	1.1	1.2	[0.0 - 3.4]
Paraeuchaeta without eggs	0.9	1.5	[0.0 - 5.1]
Crustacea	0.5	1.0	[0.0 - 3.2]
Paraeuchaeta with eggs	0.2	0.6	[0.0 - 1.7]
Amphipods	0.2	0.5	[0.0 - 1.4]

We compared the differences in the depth distribution between night and day and between groups, using a linear mixed model with depth (square root transformed) as dependent factors, species and time of day (Day, Night) as independent factor, and tow nested in sampling effort as random factor. We also allowed for an interaction between time of day and species group. In addition, we investigated what appeared to be surface avoidance behavior by calculating for each tow the depth below which 75% of the population was found, and testing the differences between day and night using an ANOVA. We also tested whether light level at which the individual copepods were found differed between day and night by using a Kruskal-Wallis rank sum test.

The copepod group was dominated by copepodites and adults of *Calanus* species. In this region, three *Calanus* species dominate: *Calanus finmarchicus*, *C. glacialis* and *C. hyperboreus* (Conover 1988, Nielsen and Hansen 1995, Madsen et al. 2001, Swalethorp et al. 2011). The size range of these copepods is wide with copepodites and adults *C. finmarchicus* and *C. glacialis* ranging between 1900 μm and 4400 μm in prosome length, while the larger *C. hyperboreus* can grow up to 7400 μm in prosome length (Frost 1974, Hirche 1997, Nielsen and Hansen 1995, Madsen et al. 2001). The three species are morphologically similar, and size alone is not enough to distin-

guish them. For *C. finmarchicus* and *C. glacialis* there is also stage specific overlap in size, and identification with high accuracy requires genetic analysis (Lindeque et al. 1999, Gabrielsen et al. 2012). However, individuals with a prosome length larger than 4400 μm could be identified as late copepodid stages of *C. hyperboreus*. Individuals smaller than this could be copepodites or adult stages of *C. finmarchicus*, *C. glacialis* or early copepodite stages of *C. hyperboreus*. We did not aim to distinguish stages in our analyses of the photos, although this would have been possible for some of the photos. Individual size can determine the motivation for DVM and the overall positioning in the water column. We therefore measured prosome length within the *Calanus* group whenever possible (i.e. when prosome was aligned parallel to the image plane), using the software ImageJ (Rasband 1997). The measurements were converted to micrometers using the known pixel size (1 pixel=23.4 μm).

For the *Calanus* spp., the role of length on the depth distribution was analyzed using a generalized additive model (GAM). The best model was selected based on the Aikaike information criteria (AIC, Akaike 1974), including models with "time of day" and "length" as fixed factors, and "depth" as dependent factor. We allowed for models having an interaction between depth and length, and controlled for differences between the sampling occasions (Day 1 and 2, Night 1 and 2) by including sampling effort as a random factor. The depth data was square root transformed prior to the analysis to meet the normality requirement. We restricted our analyses to the copepod length interval between which we had both day and night data (1621 - 5722 μm). All statistical analyses were carried out in R v3.0.1 (R Core Team 2013), and with the package "mcgv" (Wood 2006) for general additive models.

2.3 Results

2.3.1 Physical conditions

The surface light intensity at noon on Day 1 (1230 μmol photons s^{-1} m^{-2}) was almost three times lower than on Day 2 (3400 μmol photons s^{-1} m^{-2}), due to cloud cover on Day 1 (Fig. 2.1). Underwater light intensity decreased exponentially with depth with a light attenuation coefficient of 0.26 m^{-1} (R^2=0.97). The relationships between depth, fluorescence and salinity were similar across the three sampling events (Fig. 2.3). As expected at this time of year, there was a marked peak in phytoplankton biomass in the upper 25 to 50 meters (Fig. 2.3 a). Water temperature was increasing with depth, from approximately -1.5℃ at the surface to almost 4.0℃ at 300 m depth (Fig. 2.3 b). The thermocline was weak with an upper limit at ∼50 m, while salinity increased gradually with depth (Fig. 2.3 c).

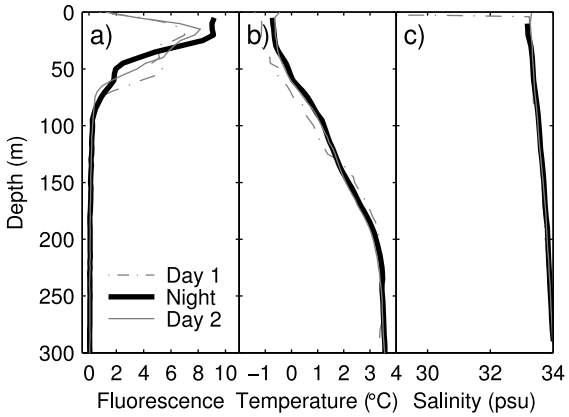


Figure 2.3: Fluorescence (a), temperature b) and salinity c) on the sampling site for Day 1 (dashed gray line), the night (Night 1a and 1b combined, bold black line) and Day 2 (gray line). The measurements were made by the CTD fitted on the VPR, except for the salinity on Day 1, when measurements were made by the CTD cast prior to the VPR sampling

2.3.2 Zooplankton community composition, abundances and migration

Fecal pellets were the most abundant particle type in our sampling (1.6 x 10^5 m^{-2}), and copepods constituted the most abundant animals (6.2 x 10^4 m^{-2}) with mainly *Calanus* spp. (Table 2.2). Due to their size, fecal pellets probably mostly originated from euphausiids and can be a proxy for their behavior, but for the rest of the analysis we focus on the animals themselves. For each group, the exact depth and time for every category of animals observed can be found in the Appendix 2.A (Fig. 2.A.1 and Fig. 2.A.2). For the most abundant animal groups, the depth distribution differed between groups, with some groups showing clear signs of DVM (e.g. euphausiids), whereas others did not (e.g. ostracods; ANOVA over *Calanus* spp., *Metridia* spp., ostracods and euphausiids: interaction time*species: $F_{(3,593)} = 5.2$, p =0.002, Fig. 2.4). Copepods were present in most parts of the water column during both day and night, but aggregated at certain depth levels as highlighted in Fig. 2.5 a. This group mainly consisted of *Calanus* spp. and to a lower extent of *Metridia* spp., with the latter one found deeper than the *Calanus* spp.. Most of the ostracods were also found in deep water (> 150 m) during both day and night. The euphausiids performed very clear DVM and were found approximately 100 meters shallower during night (∼20 m) than day (∼150 m; Fig. 2.4 and 2.5).

Copepods were found deeper at day than at night (ANOVA, $F_{(1,15)} = 82.9$, p<0.0001; Fig. 2.6). This is a result of an apparent surface avoidance behavior. The depth below which 75% of the copepods were found was 91±

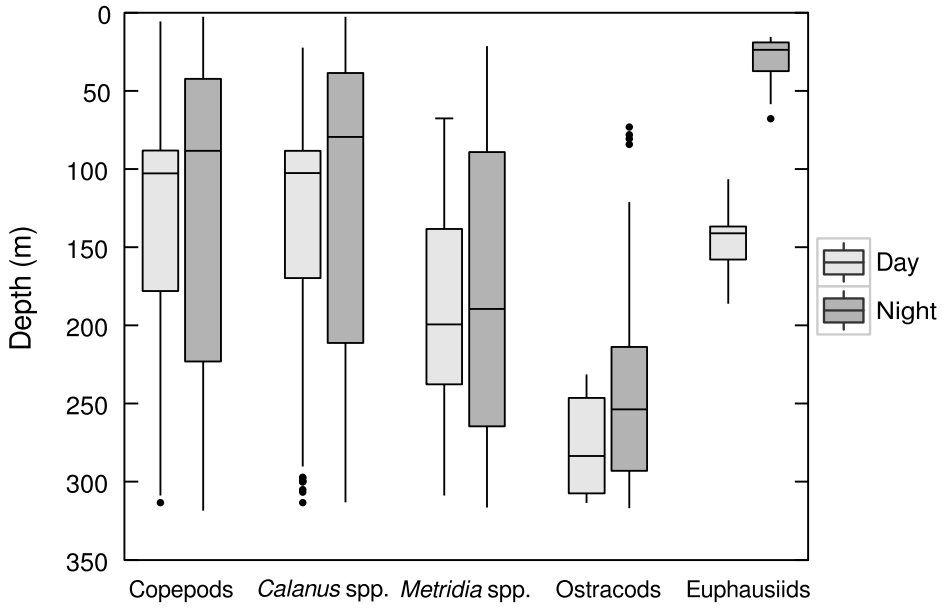


Figure 2.4: Boxplot showing the depth distribution of groups with at least 25 observations, and separated by day (light gray) and night (dark gray)

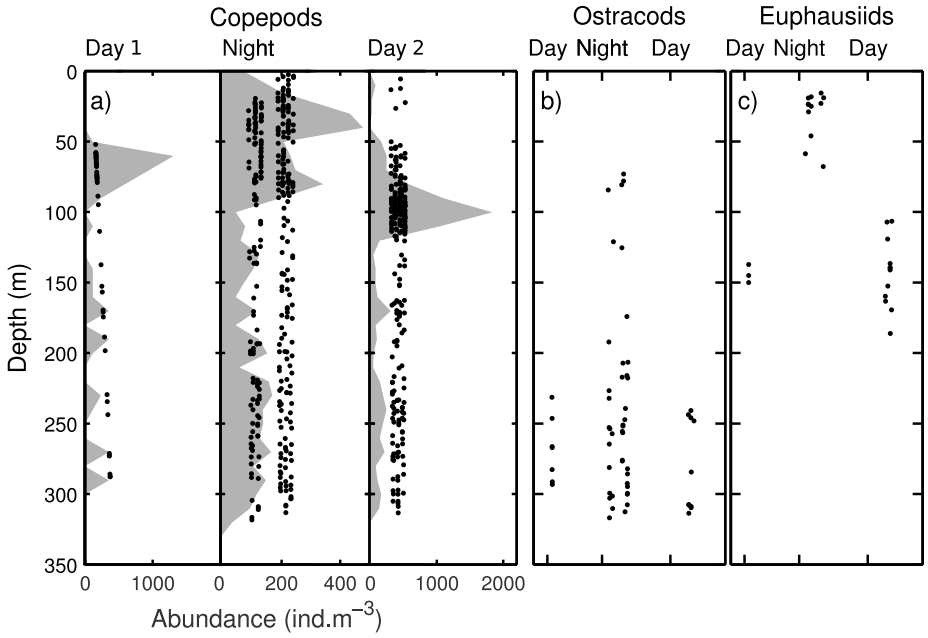


Figure 2.5: Position (dots) and abundance in 10 m depth bins (gray shaded area) of all copepods (a), ostracods (b) and euphausiids (c) by depth and time (Day 1, Night 1a and 1b combined and Day 2). Each dot represents an individual observation

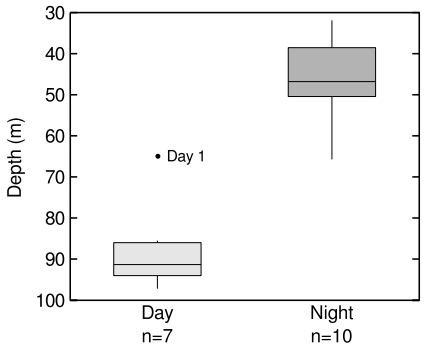


Figure 2.6: Boxplot of the depth below which 75% of the copepods where found per sampling tows. This represents the surface depth layer that most of the population avoid during day and night. The out-lier at 65 m during the Day is the sampling made during Day 1, while the rest of the Day's box represent the 6 tows sampled during Day 2

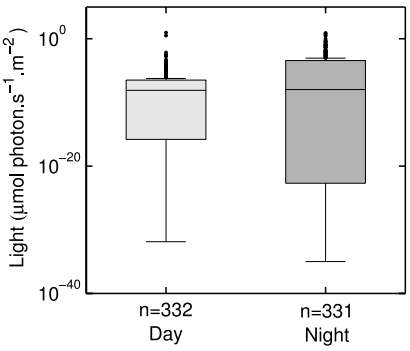


Figure 2.7: Boxplot showing how much light the copepods are exposed to at their depth position during day and night. For further explanation refer to main text

4 m (n=6) during day tows, and 46 ± 10 m (n=10) during night tows. The single tow from Day 1 (at 65 m depth) differed from all the tows of Day 2 as indicated in Fig. 2.6. This suggests that copepods were avoiding a larger depth layer during Day 2, when the light intensity at the surface was higher than during Day 1. Thus, we tested for a difference in the light level at the depths where the copepods were mainly found. The light level below which 75% of the population was located was 5.6 x 10^{-5} μmol photon s^{-1} m^{-2} during Day 1, and 1.5 x 10^{-7} μmol photon s^{-1} m^{-2} during Day 2. These light levels were similar during the night (7.4 x 10^{-5} μmol photon s^{-1} m^{-2}, Kruskal-Wallis rank sum test: $\chi^2_1 = 0.1481$, p-value = 0.70). When looking at individual behavior, the distribution of individuals as a function of light level at day versus night reveal that during daytime some seemingly "risk-taking" individuals were found at shallow depths with high light levels (Fig. 2.7).

2.3.3 Length vs depth distribution in the *Calanus* group

Calanus body size was found to influence depth distribution and the extent of DVM, with smaller individuals performing more extensive DVMs than larger individuals (the GAM model with the highest explanatory power was the one allowing for two different smooth terms for day and night, and

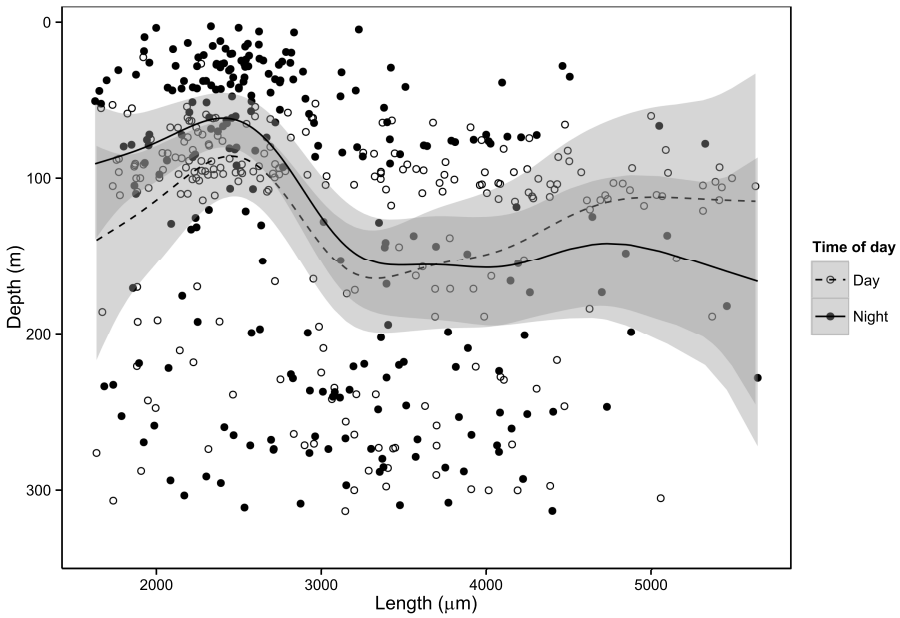


Figure 2.8: Prosome length of *Calanus* spp. during day (open symbols) and night (filled symbols). The fitted general additive model is shown by whole line for the day, and in dashed line for the night, with their standard deviations (gray shading)

included time of the day as a fixed factor, cf. Appendix 2.B, Table 2.B.1). The day and night smooth terms were significant, and the intercept of night was significantly different from the intercept of day. Fig. 2.8 shows the model fit for day and night. Although the model only explains 21.1% of the variation, it indicates that the smaller *Calanus* spp. show a DVM pattern. For the bigger *Calanus* spp. such a clear upward movement was not seen, however, the few data points did not allow for a conclusion on any pattern. During the day, most *Calanus* spp. individuals, independent of their size, accumulate at 100 meters (Fig. 2.8).

2.4 Discussion

We have shown the diversity of DVM behavior that can be found in the zooplankton community of a Sub-Arctic shelf ecosystem. Specifically, euphausiids displayed clear DVM, ostracods stayed in the deep habitat and the copepods performed DVM but with some variability. We observed a clear surface avoidance by copepods during day-time, accompanied with a long span of day-time depth locations once below the surface zone. The migration of the most abundant copepod genus (*Calanus* spp.) seems to

be size dependent, with the smaller individuals performing clear migration whilst the larger individuals stayed mostly at depth.

2.4.1 Advantages of VPR for the study of DVM

One of the advantages of utilizing a video plankton recorder (VPR) for pelagic ecology is the ability to combine concurrent measurements of environmental data (fluorescence, salinity, temperature, depth) with the precise position of individuals at any given time of sampling. This information is crucial when investigating both inter-specific and intra-specific behavioral strategy. For example, during the second day, all copepods were found below 50 m, except for five individuals which were observed at shallower depths (Fig. 2.7), feeding on the phytoplankton bloom (green guts could be seen from the photos). The high-risk behavior of these individuals could potentially be explained by starvation (Gauld 1953, Pearre 2003). By using the VPR it is also possible to study the fine scale spatial position of individuals, which is impossible when individuals are integrated over 50 m or longer as is the case with many net sampling systems. As pointed out by Pearre (2003), information of this kind is essential if one wants to understand the causes and effects of DVM. Furthermore, the pictures taken are of good quality and information on the properties of individuals, like size and coloration can in many cases be extracted from them (e.g. Baumgartner et al. 2011). In this study we focused on copepods, and from the images we could, in many cases, identify genus and measure prosome length. Although our focus, due to its low abundance, was not on *Pseudocalanus* spp., we could clearly see when they were carrying eggs or not whilst they tend to loose them in nets (Corkett and McLaren 1979). We could also see green colored algae filled guts, and lipid stores in the copepods. Finally, we could calculate the amount of light the individuals were exposed to, using the precise depth position and time of sampling (e.g. Appendix 2.C, Fig. 2.C.1).

2.4.2 DVM strategies of zooplankton in Disko Bay

Zooplankton adopt DVM in the presence of food and when light levels are sufficient to allow visual predators to hunt effectively (Pearre 2003). This is the case during our study as the peak of fluorescence was found at 25 to 50 m depth, and fish (not studied by us) can be assumed to be an abundant predator on copepods in the system (e.g. Arctic cod *Boreogadus saida*, sand lance *Ammodytes* spp. and Atlantic poacher *Leptagonus decagonus*, Munk et al. 2000, Hamilton et al. 2003, Stenberg 2007). According to the predator avoidance hypotheses, DVM is a beneficial strategy for zooplankton only when reduced predation risk counterbalances lost feeding opportunities. For example, using a game theory approach played between grazers and visual predators, Sainmont et al. (2013) showed that DVM is an emergent strategy

when the losses due to predation are higher than the gain provided by extra feeding during daylight hours. In Disko Bay, light levels at the surface were higher on Day 2 than Day 1 of sampling and the resulting elevated risk at shallow depth may partially explain the deeper depth distribution of the copepods on Day 2 compared to Day 1. By avoiding the topmost 65 and 90 m during day-time (Day 1 and Day 2, respectively), the copepods could reduce the risk of visual predation (light) but were consequently some distance away from the peak concentrations of phytoplankton food.

Among the *Calanus*, we found that small individuals performed DVM with a wide range of variability, modulated by ambient light. The variability in the depth distribution could potentially be explained by individual state, for example stomach fullness, energy reserves or differences in life-history strategies between the three *Calanus* species (Hays et al. 2001). It has also been suggested that copepods could make ascents to feed in the phytoplankton layer and sink whilst digesting (Lopez and Huntley 1995, Pearre 2003). Furthermore, some copepods were found higher in the water column than the peak of phytoplankton bloom, which seems sub-optimal as it is more risky (higher light level). However, competition for food at the peak food concentration is likely to be high, and copepods may therefore disperse over the phytoplankton layer to avoid intra-specific competition for food (cf. ideal free distribution, Fretwell 1972). Individual dispersion could also be a strategy against tactile predators (such as chaetognaths, amphipods and ctenophores that were observed in this study), or filter-feeding whales, which capture their prey during the day as well as night (Hays 2003, Ohman 1990).

DVM was not evident for larger individuals, that generally were found deeper than smaller individuals, which has also been observed in other studies (e.g. Wiebe et al. 1992, De Robertis et al. 2000). Thus, food availability in the surface layers is not affecting their depth distribution.

Small individuals of the *Calanus* spp. group are assumed to be copepodite stages or adult *C. finmarchicus*, *C. glacialis*, or young copepodite stage of *C. hyperboreus*, while individuals larger than 4.5 mm could only be late copepodite stages or adult *C. hyperboreus*. Individuals of larger size will be more easily detected by visually hunting predators. They also generally have a longer life span and have therefore more to lose in terms of survival (Pasternak et al. 2001). Furthermore, *C. hyperboreus* is a capital breeder (cf. Varpe et al. 2009) that spawns in winter and early spring (Hirche 1997, Swalethorp et al. 2011, Conover et al. 1988). An essential part of their life history is thus to accumulate and store reserves during the phytoplankton bloom period, but also to survive until the next winter (e.g. Falk-Petersen et al. 2009, Varpe 2012). They may, therefore opt for safer behavior, which could explain a deeper distribution. Furthermore, they may feed on detritus or marine snow at depth (Möller et al. 2012, Alldredge and Silver 1988, Hansen et al. 1996). An income breeding species with a shorter life cy-

cle, such as *C. finmarchicus* (Conover 1988), is more dependent on current food intake. They may therefore benefit from a more risk-prone behavior to achieve high growth and egg production rates. In this case, DVM is very likely a good compromise between feeding and visual predator avoidance.

Other species recorded by the VPR included euphausiids which are larger in size and have a greater swimming capability than copepods. Euphausiids revealed a clear DVM signal, with all individuals, although relatively few due to the VPR setting used, found within distinct depth intervals at both day and night. No euphausiids were found below 70 m during night or above 100 m during the day. Our findings correspond well to previous studies on DVM of euphausiids (e.g. Onsrud and Kaartvedt 1998, Tarling et al. 2010). Due to their large size, euphausiids are highly vulnerable to visual predators during daylight hours, and therefore it is not surprising to see all individuals avoiding the surface waters during day-time. During night-time, however, their position matched with the phytoplankton bloom layer, adding an interspecific component to the competition for food experienced by the copepods (see above).

Few comparative data on vertical distribution of ostracods exist and none for Disko Bay or western Greenland. Ostracods observed in Disko Bay were located deep in the water column during the day (220 - 300 m), and at night they extended their vertical distribution to a shallower depth (60 - 300 m). Studies from another coastal Arctic area, the waters around Svalbard, are in agreement with our findings that ostracods are a deep living group of animals. Off Svalbard, ostracod abundances are reported as highest in mid to deep water layers (200 - 600 m, Baczewska et al. 2012).

2.4.3 Effect of zooplankton DVM on higher trophic level behavior

The daily migration of zooplankton is likely to influence the behavior of their predators. Theory predicts that it is advantageous for planktivorous predators to follow the DVM pattern of their prey even though the habitat's physical conditions are not advantageous for them (e.g. lack of light to fully enjoy their visual acuity, Sainmont et al. 2013). Baumgartner et al. (2011) showed that the North Atlantic right whales (*Eubalaena glacialis*) could take advantage of copepod DVM but fish predators (e.g. sand lances, *Ammodytes* spp.) and the sei whales (*Balaenoptera borealis*) were missing feeding opportunity due their inability to forage at depth and in darkness. Similarly, humpback whales (*Megaptera novaeangliae*) have been observed to change their foraging diving depth diurnally to take advantages of the shallower depth of krill in the Antarctic during the night (Friedlaender et al. 2013). Disko Bay and western Greenland have large populations of marine mammals, including baleen whales which feed on copepods (Heide-Jørgensen et al. 2007), however, it is unclear if whale abundance really affects the cope-

pods vertical migration pattern in the region. Our study did not allow these interactions to be studied, but future studies should aim to test it and high spatial resolution achieved with VPR sampling will be valuable.

2.4.4 Conclusion

In conclusion, this study showed the wide variability of daily migration patterns among and within groups, as resolved to the fine scale spatial position of individuals by the VPR. The results are in agreement with the hypothesis that DVM is an adaptive behavior which increases survival by feeding at night, which is likely to increase their life-time reproduction output. Our findings suggest that smaller (and thus often younger) individuals exhibit a more risk prone behavior prioritizing food intake and growth rather than safety. Survival through the next winter may be at risk. On the other hand, larger individuals, may benefit from safer behavior, staying all the time in the deep and potentially switching food sources. VPRs have great potential in the study of individual behavior strategies, thanks to fine scale spatial resolution. VPRs can, for example, generate input data that could be used in trait-based modelling studies. Such detailed data on individuals are currently lacking and hard to obtain using traditional sampling methods as net-sampling or acoustic surveys.

Acknowledgements

The data has been collected during the PhD course sponsored by Nordforsk "Fate of the Arctic spring bloom" between April 25 to May 7, 2012 at the Arctic Station, Qeqertarsuaq, Greenland. A. Gislason and Ø. Varpe wish to thank Torkel G. Nielsen for the opportunity to teach during the course and to run a DVM project with one of the student groups, and we all thank him for organizing the course and giving us the opportunity to do this interesting study. We wish to thank the Arctic Station and the Geographical and Geological Institute from Copenhagen University for sharing their solar irradiance data collected at the Arctic station. J. Sainmont and Ø. Varpe also thank Mark Ohman for interesting discussions around an earlier draft of this work and André W. Visser for his support and advices. We thanks Mark Payne for statistical advices. Ø. Varpe was supported by The Research Council of Norway through project CircA. This work was supported by the Greenland Climate Research Centre and the Centre for Ocean Life, a VKR center of excellence funded by the Villum foundation.

Appendix

2.A Day/night individual positions

We present our complete data set of plankton groups with their precise depth positions (Fig. 2.A.1) and with the cumulative percentage from bottom to the top of the water column (Fig. 2.A.2)

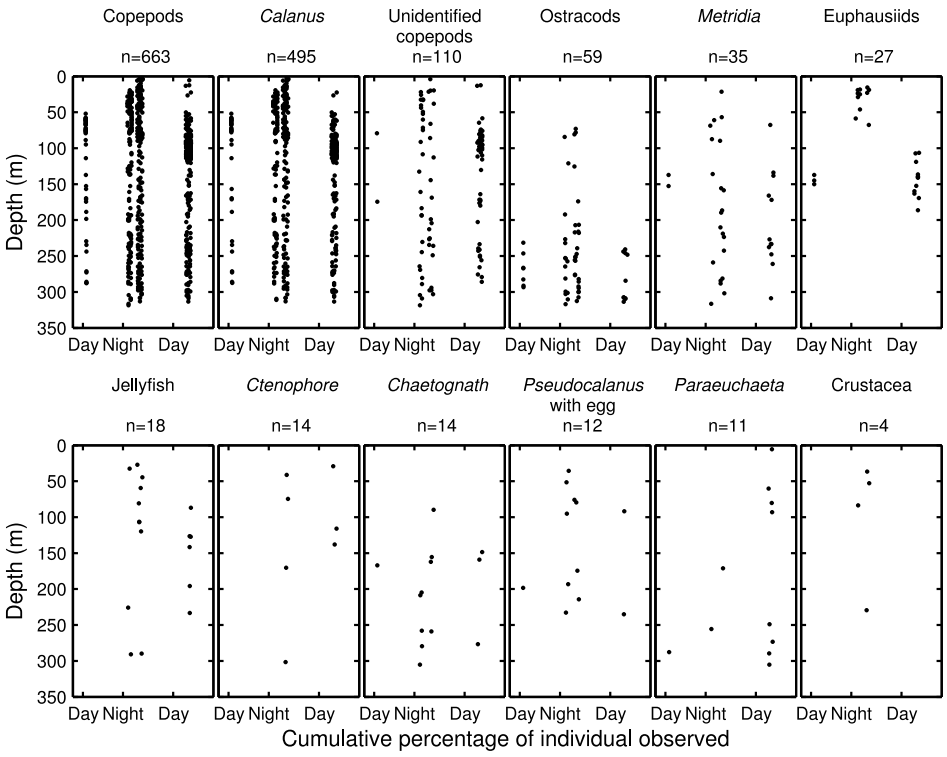


Figure 2.A.1: Position of individuals observed by category, depth and time (Day 1, Night 1a and 1b and Day 2). "n" is the total number of observations

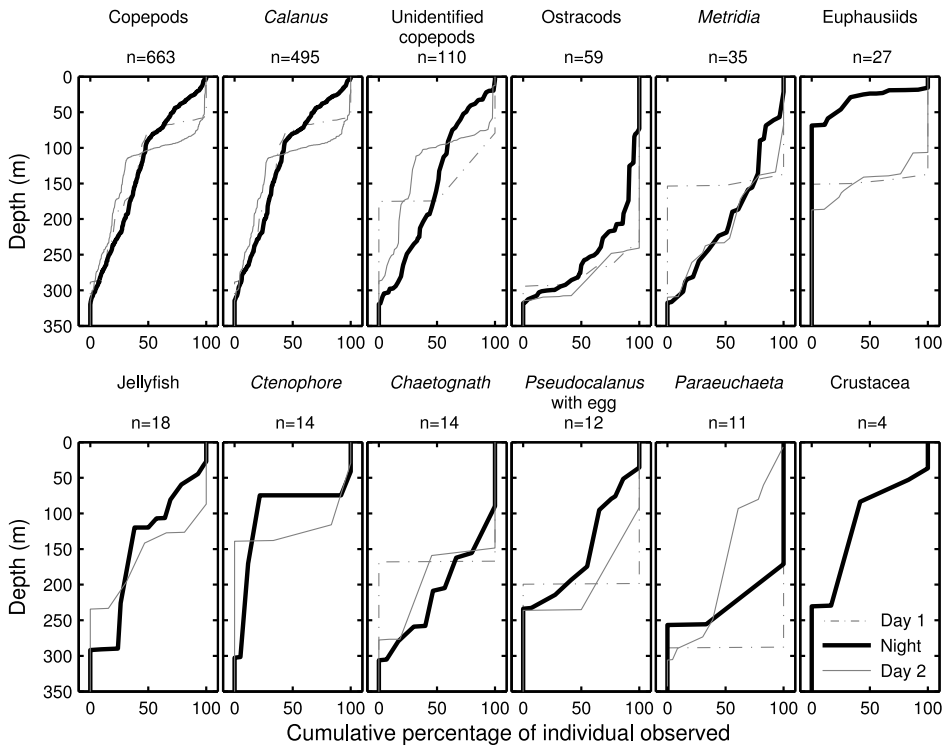


Figure 2.A.2: Cumulative frequencies of individual observations by category and depth. "n" is the total number of observations. The black line represents the average distribution at night, the dashed gray line during Day 1, and the gray line during Day 2

2.B GAM model

The table summarizing the GAM model and selection is presented in Table 2.B.1.

Table 2.B.1: Model estimates and summary of the best fitting general additive model analyzing the depth distribution of *Calanus* spp. as a function of time and length

GAM structure: $\sqrt{\lvert\text{Depth}\rvert} \sim s(\text{Length}) + s(\text{Length, by} = \text{as.numeric(time of day} == \text{“day”)}) + \text{time of day} + s(\text{VPR number, bs} = \text{“re”}))$				
Parametric coefficients:				
	Estimate Std.	Error	t-value	Pr(> |t|)
(Intercept)	7.079	0.109	64.8	$< 2E^{-16}$ ***
time of day	3.177	0.174	18.3	$< 2E^{-16}$ ***
Approximate significance of smooth terms:				
	edf	Ref.df	F	p-value
s(Length)	6.613	7.75	13.61	$< 2E^{-16}$
s(Length):as.numeric(time of day == “day”)	1.667	1.67	188.32	$< 2E^{-16}$
s(VPR number)	0.129	2.00	0.07	0.34
R-sq.(adj) = 0.196	Deviance explained = 21.1%			
GCV score = 11.725	Scale est. = 11.492		n = 489	

2.C *Calanus* spp. light exposure

We report on the light exposure of *Calanus* spp. as a function of their prosome length (Fig. 2.C.1). The light exposure is calculated as a function of the surface light intensity at the time of sampling and the depth at which the individuals were found, assuming an exponential light decrease in the water column.

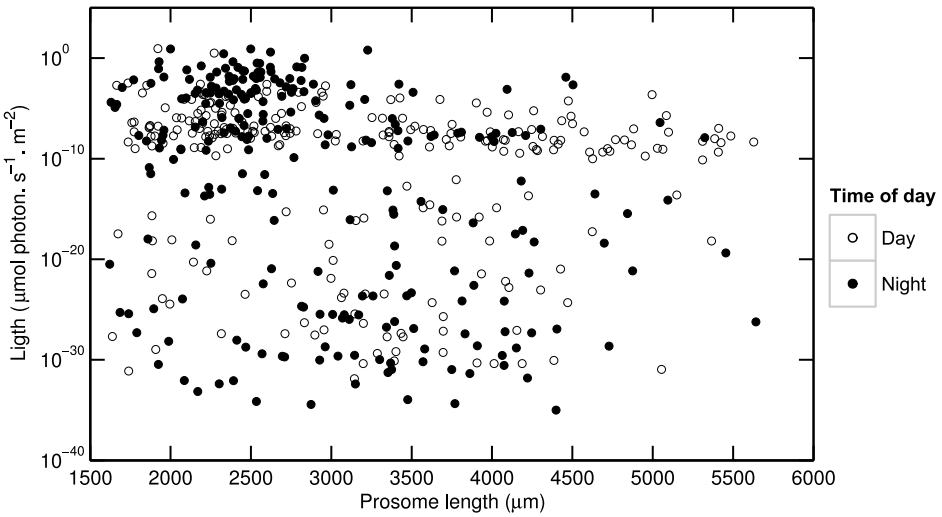


Figure 2.C.1: The exposure of *Calanus* spp. to light during Day 1 and Day 2 (open symbols) and during Night 1a and 1b (filled symbols) as a function of prosome length. The light level is calculated for each individual as a function of the light intensity at the surface at the time of observation $I_0(t)$, the light attenuation coefficient (α=0.26), and the depth of the individual according to equation 2.1

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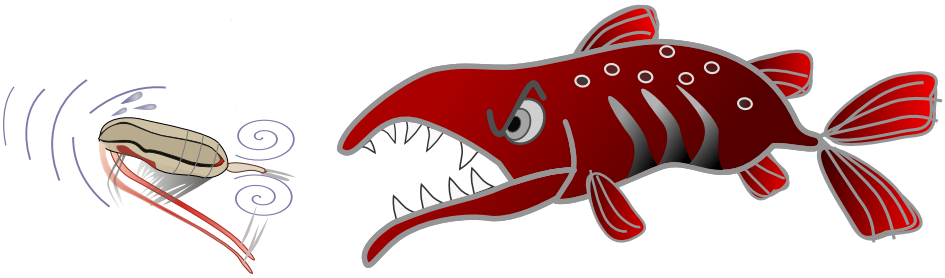
Chapter 3

Diel vertical migration arising from an habitat selection game

Sainmont J., Thygesen, U. H., and Visser, A. W. (2012). *Theoretical ecology*, 6(2):241–251



Theor Ecol
DOI 10.1007/s12080-012-0174-0

ORIGINAL PAPER

Diel vertical migration arising in a habitat selection game

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Received: 18 July 2012 / Accepted: 27 September 2012

Abstract Predator and prey react to each other, adjusting their behavior to maximize their fitness and optimizing their food intake while keeping their predation risk as low as possible. In a pelagic environment, prey reduce their predation mortality by adopting a diel vertical migration (DVM) strategy, avoiding their predator during their peak performance by finding refuge in deep layers during daylight hours and feeding at the surface during the night. Due to the duality of the interaction between prey and predator, we used a game theory approach to investigate whether DVM can be a suitable strategy for the predator as well as the prey. We formulated three scenarios in plankton ecology in order to address this question. A novel finding is that mixed strategies emerge as optimal over a range of the parameter space, where part of the predator or prey population adopts a DVM while the rest adopt one or other "sit and wait" strategies.

Keywords Predator–prey interaction · Habitat selection · Game theory · Diel vertical migration · Zooplankton

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Introduction

One of the most conspicuous features of marine pelagic ecosystems is the daily vertical migration exhibited by large numbers of organisms including fish (Beamish 1966), krill (Bollens et al. 1992; Zhou and Dorland 2004), jellyfish (Kaartvedt et al. 2007), copepods (McLaren 1963; Hays et al. 2001; Bollens and Frost 1989), and protists (Eppley 1968). Indeed, it has been argued that this vertical migration constitutes one of the largest concerted movements of biomass on earth (Hays 2003; Angel and Pugh 2000). This migration is not only important in shaping trophic interactions in the marine ecosystem, but it also contributes to the biological pump, influencing the rate at which carbon is drawn down from the atmosphere and sequestered in the deep ocean (Steinberg et al. 2000; Ducklow et al. 2001), with implications for global climate.

The imperative for vertical migration can be largely found in predator–prey interactions (Zaret and Suffern 1976). As in all predator–prey interactions, both predators and prey attempt to maximize their food intake (to fuel growth and reproduction) while at the same time seeking to minimize their mortality due to predation. In pelagic waters, prey can find refuge in deeper, darker waters, where the predator's visual acuity is reduced (Aksnes and Giske 1993; Fortier et al. 2001). Therefore, the diel vertical migration (DVM) of zooplankton between the surface layers at night and the deeper waters during the day has largely been attributed to the trade-off between the availability of food and the necessity of avoiding predators (Lampert 1989; Dill 1987).

Diel vertical migration of zooplankton has been widely studied in fjords (Frost 1988; Bollens et al. 1992; Onsrud and Kaartvedt 1998), shelf seas (Krause and

Published online: 08 November 2012

Radach 1989; Irigoien et al. 2004; Durbin et al. 1995), as well as open ocean systems (Hays 1996; Hattori 1989). In general, three patterns emerge: normal migration, reverse migration, and no detectable migration. These different patterns may be exhibited by the same population at different times. For instance, in the population of the copepod *Pseudocalanus newmani* in Dabob Bay, Washington, USA, different DVM patterns are correlated with the presence or absence of their predators (the copepod *Euchaeta elongata*, the chaetognath *Sagitta elegans*, and the euphausiids *Euphausia pacifica*) as well as the abundance of planktivorous fish (Ohman 1990) which target these predatory zooplankton in turn. In the same area, seasonal and interannual variation in the migratory behavior of the copepod *Calanus pacificus* yield significantly different mortality rates in migrating and nonmigrating copepods (Frost 1988). Further, while in general, populations move vertically according to some daily rhythm, it is also conspicuous that not all individuals do the same (Hays et al. 2001). Differing proportions of populations may migrate or remain in residence in surface or deep habitats. Indeed, detailed measurements of the vertical migratory behavior of individual jellyfish *Periphylla periphylla* (Kaartvedt et al. 2007) show asynchronous migrations by individuals sporadically throughout the day and night. These differences in migratory behavior have been ascribed to the different states (e.g. age, size, maturity, gut-fullness, and reserves) of individuals (Hays et al. 2001) and the subsequent trade-offs these individuals are faced with in maximizing their fitness.

Different methods to model the trade-offs inherent in DVM have been proposed over the years, such as dynamic programming (Mangel and Clark 1986; Fiksen and Giske 1995; Fiksen et al. 1998; Titelman and Fiksen 2004), life history theory (McLaren 1963), and genetic algorithms (Fiksen 2000; Eiane and Parisi 2001; Strand et al. 2002). However, most of these predator–prey interaction studies focused almost entirely on the prey, with the assumption that only the prey adapts its behavior. Lima (2002) argued that the entire predator–prey interaction should be taken into account, and that the predator adapts its behavior to the prey as much as vice versa. The predators should thus be able to follow the prey and react to their potential behavioral adjustments in order to maximize their hunting activity. Game theory has emerged as one of the best approaches for investigating how prey and predator interact, because it considers the characteristics and goals of both actors. While dynamic programming, life history theory, and genetic algorithms optimize individual's behavior on long time scale, game theory often focus on short time scale; the day-to-day business of foraging in a risky environment. Finally, as a practical matter, game theory methods involve a low computational cost.

Game theory was introduced in ecology as the ideal free distribution (Fretwell and Lucas 1969), and Iwasa (1982) was the first to use game theory to explain the interaction between predators and prey and their distribution between two habitats. However, his results were not evolutionarily stable (Gabriel and Thomas 1988) and did not include DVM as a possible strategy. Gabriel and Thomas (1988) proposed a model that reaches the evolutionary stable state, but did not described the predator behavior. Afterward, Hugie and Dill (1994) presented a game theory using populations of fixed size and studied the interference and dilution effects in habitat choice, without including the DVM strategy. Later, Luttbeg and Sih (2004) used genetic algorithms to show that the relative importance of intra and interspecific competition is ruled by the fitness calculation, while Flaxman and Reeve (2006) explored the reasons for deviations from ideal free habitat selection.

As in the Hugie and Dill's study (1994), we investigate an inter- and conspecific game where prey and predator can choose between staying at the surface or going into the deep, and we add the possibility of a DVM strategy. We explore under which conditions DVM is the best strategy for the predator or the prey and, by contrast, under which conditions staying in one environment is the best strategy. To this end, three scenarios were analyzed: (1) Only the prey could perform DVM; (2) Prey and predator could both perform DVM; and (3) Presence of a top predator in the system. Some examples from the literature are used to illustrate the model.

Method

We consider a prey population (N) and a predator population (P) in a water column, which is divided into a surface habitat (S) and a deep habitat (D). Each individual chooses between the two habitats in order to maximize its fitness. Three strategies are investigated: staying at the surface (S), staying in the deep (D), or performing a DVM, by seeking refuge in the deep layer during the day and ascending to the surface at night (m). Migrating individuals are in the deep when it is light, which it is a fraction σ of the time, and at the surface when it is dark, a fraction $1-\sigma$ of the time. We assume that the population size remains constant

and focus on the distribution of individual between strategies at a given time. The proportion of individuals that adopt each strategy is denoted as N_S, N_D, and N_m for the prey, and as P_S, P_D, and P_m for the predators:

$$\begin{cases} N_S + N_D + N_m &= 1 \\ P_S + P_D + P_m &= 1 \end{cases} \tag{1}$$

We evaluate fitness as the difference between specific growth rate and mortality rate. We choose a type I functional response for simplicity, assuming that the predator remains under-satiated at all times. For the prey, the specific growth rate is density independent and equals λ_S for an individual which adopts the "surface" strategy S, and λ_D for an animal which adopts the "deep" strategy D. A migrating prey individual experiences a time-averaged growth rate $\sigma\lambda_D + (1-\sigma)\lambda_S$. In turn, a prey individual's instantaneous predation risk is found as $V \cdot P$, where P is the proportion of predators present in the prey's habitat at this instant, and the factor V is denoted predator voracity. This voracity differs between night and day and between the surface and the deep, and is an aggregate parameter which is affected by total predator abundance and relative habitat sizes, relative speed of movement between predator and prey, and detection distance. Time-averaged predation risks will be computed in the following in three different scenarios.

For the predator, the instantaneous growth rate is proportional to $V \cdot N$, where V is the local voracity and N is the fraction of prey occupying the predator's habitat.

Note that the fitness of an individual is independent of its conspecifics and a linear (strictly, affine) function of the densities of the other species; i.e., we make the same simplifying assumptions of density independence and Holling type I functional response as in the classical Lotka–Volterra model of population dynamics.

Scenario 1: Only the prey can perform DVM

In this first scenario, the preys are able to choose the DVM strategy, while the predators only have the choice between remaining in the surface or the deep habitat (i.e., we enforce $P_m \equiv 0$). The fitness of a prey in the deep is the difference between growth rate and predation mortality, i.e., $F_{N_D} = \lambda_D - V_d P_D$. A prey which stays at the surface has a growth rate of λ_S and encounter surface predators which have a time-averaged voracity of $\sigma V_l + (1-\sigma)V_d$ (voracity V_l in presence of light, and V_d in darkness). Prey performing DVM are always in the dark and therefore encounter predators with constant voracity V_d, but with a time-averaged relative abundance $\sigma P_D + (1-\sigma)P_S$. In summary, the fitness of prey adopting the different strategies are:

$$\begin{cases} F_{N_S} = \lambda_S - (\sigma V_l + (1-\sigma)V_d)P_S \\ F_{N_D} = \lambda_D - V_d P_D \\ F_{N_m} = \sigma(\lambda_D - V_d P_D) + (1-\sigma)(\lambda_S - V_d P_S) \end{cases} \tag{2}$$

Similarly, a surface predator has a voracity V_l in the day-time where it encounters prey with abundance N_S, and a voracity V_d in the nighttime where the prey abundance is $N_S + N_m$. A predator in the deep has constant voracity V_d and experiences a time-averaged prey abundance $N_D + (1-\sigma)N_m$. In summary, the fitness of the two predator strategies are:

$$\begin{cases} F_{P_S} = (\sigma V_l + (1-\sigma)V_d)N_S + (1-\sigma)V_d N_m \\ F_{P_D} = V_d N_D + \sigma V_d N_m \end{cases} \tag{3}$$

Scenario 2: Prey and predator can both perform DVM

In this scenario, both prey and predator may perform a DVM. That is, we allow the predator to match the prey distribution daily, as suggested by Lima (2002). Predators performing DVM forage in the surface at night, in the deep during daytime, and all day long on the vertically migrating prey (Eq. 4). Since migrating predators are always in the dark, their voracity is constant V_d. From the point of view of the prey, migrating predators gives rise to an extra term in the predation risk (Eq. 2): $(1-\sigma)V_d P_m$ for surface prey, $\sigma V_d P_m$ for deep prey, and $V_d P_m$ for migrating prey. Thus, the fitness of prey strategies become:

Prey:

$$\begin{cases} F_{N_S} = \lambda_S - (\sigma V_l + (1-\sigma)V_d)P_S - (1-\sigma)V_d P_m \\ F_{N_D} = \lambda_D - V_d P_D - \sigma V_d P_m \\ F_{N_m} = \sigma(\lambda_D - V_d P_D) + (1-\sigma)(\lambda_S - V_d P_S) - V_d P_m \end{cases} \tag{4}$$

Predator:

$$\begin{cases} F_{P_S} = (\sigma V_l + (1-\sigma)V_d)N_S + (1-\sigma)V_d N_m \\ F_{P_D} = V_d N_D + \sigma V_d N_m \\ F_{P_m} = (1-\sigma)V_d N_S + \sigma V_d N_D + V_d N_m \end{cases} \tag{5}$$

Scenario 3: Presence of a top predator in the system

In the last scenario, we investigate the impact of a third trophic level on top of the predator–prey system considered so far. This top predator is only allowed to forage on the intermediate predator and is assumed to stay at the surface ($T_S = 1$) all the time, but is given different foraging efficiencies in the day and the night. The fitness of prey in the scenario is that in the previous scenario, i.e., Eq. 4. For surface and migrating intermediate predators, a predation risk is amended:

Predator:

$$\begin{cases} F_{P_S} = & (\sigma V_l + (1-\sigma)V_d)N_S + (1-\sigma)V_d N_m \\ & -(\sigma W_l + (1-\sigma)W_d)T_S \\ F_{P_D} = & V_d N_D + \sigma V_d N_m \\ F_{P_m} = & (1-\sigma)V_d N_S + \sigma V_d N_D + V_d N_m \\ & -(1-\sigma)W_d T_S \end{cases} \quad (6)$$

Since top predators have fixed strategies, their fitness does not influence model results, but we include it for completeness:

$$F_{T_S} = \sigma W_l P_S + (1-\sigma)W_d(P_S + P_m) \quad (7)$$

Solution

The fitness functions define a noncooperative game, where individuals play against individuals of their own species as well as individuals of the other species. To solve this game, we identify the Nash equilibrium, where no individual can gain an advantage by changing strategy. The Nash equilibrium is found numerically by solving the replicator equation until steady state (Schuster and Sigmund 1983; Hofbauer and Sigmund 2003); see Appendix for details.

Results

Our primary interest was to investigate the migration patterns emerging as a result of differing factors contributing to the fitness trade-offs or the various actors. To facilitate intercomparison, the model was set up so that the prey's available food in the deep, predation efficiency in the deep, and top predator efficiency in the dark were all assumed to stay constant ($\lambda_D = 0.2$, $V_d = 0.1$, and $W_d = 0.05$). The simulations were set for a daylight hour proportion $\sigma = 0.65$ per day. The effect of changes in prey's growth rate (λ_S), in predation voracity (V_l), and the top predator efficiency in the surface and in light hours (W_l) were investigated in the different scenarios.

Scenario 1: Only the prey could perform DVM

Prey had the choice between staying at the surface, in the deep or performing a diel vertical migration (i.e., staying at the surface during the night and in the deep during the day). The DVM strategy for the prey was advantageous so long as the predators' voracity was relatively high compared to the prey's growth rate (Fig. 1). In the opposite situation, i.e., when the growth rate at the surface was very high compared to the predator voracity, the prey favored the surface, no matter what the distribution of the predator was. Further, the whole prey population chose the same strategy, all remaining in the surface (low risk, high growth) or performed diel migration (high risk, low growth). In the meantime, the proportion of predators at the surface increased when the prey's growth rate (λ_S) increased (matching the observation made by Hammond et al. 2007) and all the predators remained at the surface when all the prey were there (Fig. 1). Therefore, apart from the case where all the prey were concentrated in the same habitat, the predator tend to match the prey resources and not their own resource distribution, a feature which Sih (1998) and Flaxman and Lou (2009) also observed.

Scenario 2: Prey and predator could both perform DVM

Now, predators were given the possibility of following their prey in a DVM between the deep layer during daylight hours and the surface layer at night. Although, the DVM strategy was not purely favorable for the predator, as they could not benefit from their high visual performance (they stay in the deep layer, where the light cannot penetrate during the day, and come to the surface when it is dark), the DVM strategy allowed the predators to match the prey distribution and migration. Optimal prey strategies were similar to scenario 1, with largely the whole prey population choosing the same strategy, all remaining in the surface (low risk, high growth) or performing diel migration (high risk, low growth, Fig. 2). Unlike the first scenario, the predators did not choose to remain in the deep habitat. This result can easily be understood by the absence of a migration cost and the absence of prey in this habitat at night. Unsurprisingly, when all the prey remained in the surface under high growth, low risk, so too did the predators while DVM becomes a suitable strategy for both predator and prey when food levels drop and predator performance increases. However, while the

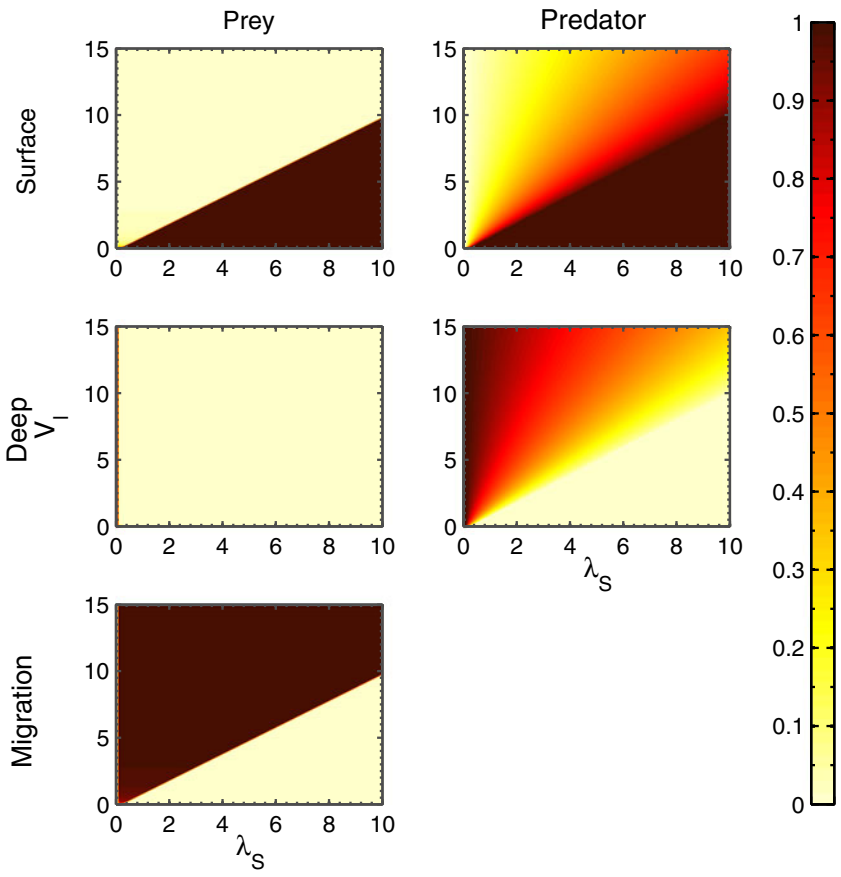

Fig. 1 Proportion of individuals in the different strategies, with the prey in the *left column* and the predators in the *right column*, in the case where the prey are the only ones able to perform the DVM. On the x-axis, we varied the prey's growth rate in the surface, and on the y-axis the daylight predator voracity. The *first row* represents the proportion of individuals that choose the strategy of staying in the surface. The *second row* shows the proportion that chose the deep strategy, and the *bottom row* represents those that chose the DVM strategy

switch in strategies for prey encompasses very nearly the whole population at once, the predator population exhibits a more mixed response with variable fractions of the population choosing one strategy or the other.

Scenario 3: Presence of a top Predator in the system

The system includes a top predator above the prey–predator system, which is assumed to forage only on the intermediate predator. Introducing a top predator into the predator–prey system opens new opportunities for the prey (Fig. 3 compared to Fig. 2), "the enemies of my enemy is a friend" situation (Fiksen 2000). The prey can now freely match their resources when the predation risk from the top predator is sufficient to deter the intermediate predator. In such circumstances, the intermediate predator will perform DVM and the prey can stay freely in the surface (see Fig. 3 and bottom right corner of each panel in Fig. 4, showing high W_I values and low V_I values). However, when the intermediate predator is more efficient than the top predator, the intermediate predator prefers to sustain the mortality risk and will divide between staying in the surface and migrating (top of the panel in Fig. 3 and bottom left corner of each panel in Fig. 4, low value of W_I). When the intermediate predators become too efficient at foraging on the prey, the preys look for refuge in the DVM strategy, leading the intermediate predator to follow them partially in their migration (top of each panel in Figs. 3 and 4).

It is interesting to observe that when the prey and intermediate predator both display mixed strategies, e.g., high voracity V_I and prey growth rate λ_S in Fig. 3, the proportions of the different strategies are determined indirectly, by the game played by the other species. For example, the proportions of the prey strategies are independent of the prey growth rate λ_S but depend only the voracity V_I of their predators (Fig. 3, top left panel). What explains this somehow counterintuitive phenomenon is that the prey proportions are determined by the requirement that the predator strategies must have same fitness: Clearly, the prey growth rate λ_S does not directly affect predator fitness and therefore does not affect prey distribution. Similarly, the proportions of predator strategies are determined by the requirement that the prey strategies have same fitness, and is therefore essentially given by the ratio V_I/λ_S, which explains the diagonal isoproportion lines in Fig. 3, top right

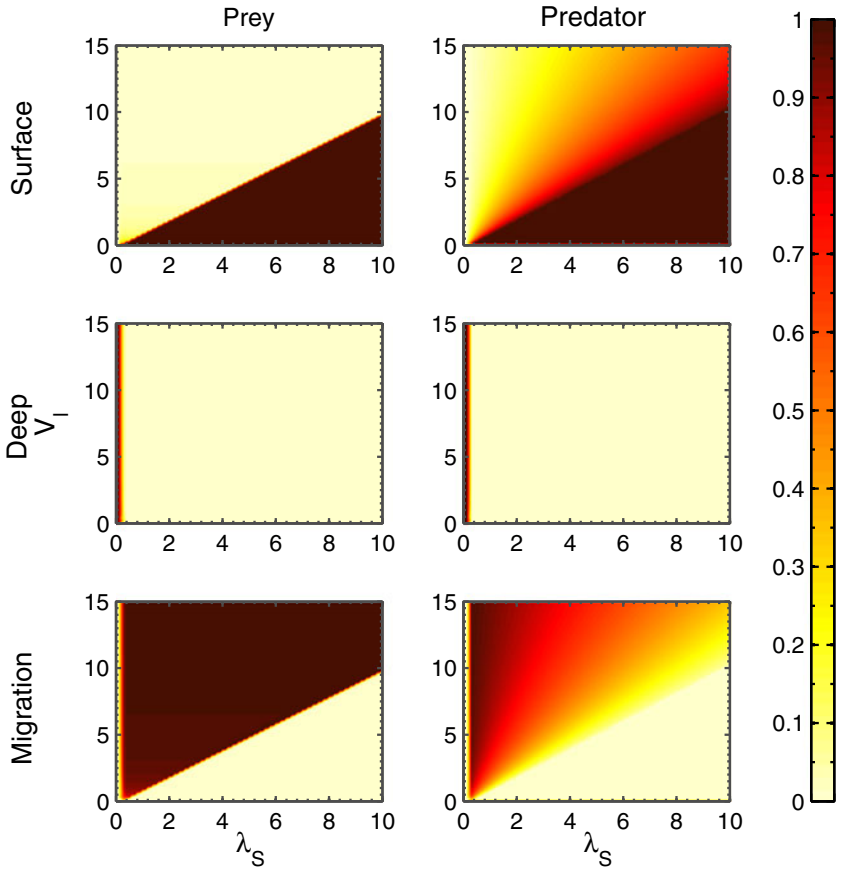

Fig. 2 Proportion of individuals in the different strategies, with the prey in the *left column* and the predators in the *right column*, in the case where prey and predators can both perform the DVM. On the x-axis, we varied the prey's growth rate in the surface, and on the y-axis the daylight predator performance. The *first row* represents the proportion of individuals that choose the strategy of staying in the surface. The *second row* shows the proportion that chose the deep strategy, and the *bottom row* represents those that chose the DVM strategy

panel. This phenomenon of indirect control is related to the well-known Lotka–Volterra equations, where the equilibrium abundance of prey is independent of its own growth rate but not independent of predator mortality (e.g., Edelstein-Keshet 2004, p. 220).

Discussion

Our game theoretic model of diel vertical migration, predicated on the fitness trade-offs incurred by predators and prey, reproduces the main features observed in nature; that prey select DVM when risk in surface waters during the day outweighs the added benefit of resource acquisition. Moreover, it predicts DVM as an optimal strategy for predators as well, when following migrating prey provides an added benefit either in feeding opportunity (scenario 2) or in mitigating their own predation risk (scenario 3). This coupling of DVM behavior between trophic levels echoes the "cascading migration" concept forwarded by Bollens et al. (2011). While the proximate causes of DVM may be more complex than presented here (e.g., temperature effects on metabolic rates (Fiksen and Giske 1995), turbulence, risk, and feeding opportunities (Visser et al. 2009)), the modeling framework presented here provides a means of assessing evolutionary stable strategies across trophic guilds. A particular feature of the model is the emergence of mixed strategies, where parts of the population assume different strategies. This may at first seem puzzling, as there is no inherent density dependence included in the various fitness trade-offs. There are, however, functional density dependencies mediated by trophic interactions; DVM in prey is dependent not just on the performance of predators, but the proportion of the predator population adopting a specific strategy. When predators come under the risk of predation themselves, mixed strategies become apparent in the prey population as well. That is, mixed strategies are a feature of the underlying interactions, and not just due to demographic variance and the somewhat different trade-off options experienced by individual members of the population (Ohman 1990).

The king penguins *Aptenodytes patagonica* in the Kerguelen islands are a good example of inter- and conspecific competition between predators and prey. Studies of the depth dive of the king penguins have shown that they perform deep dives during daylight

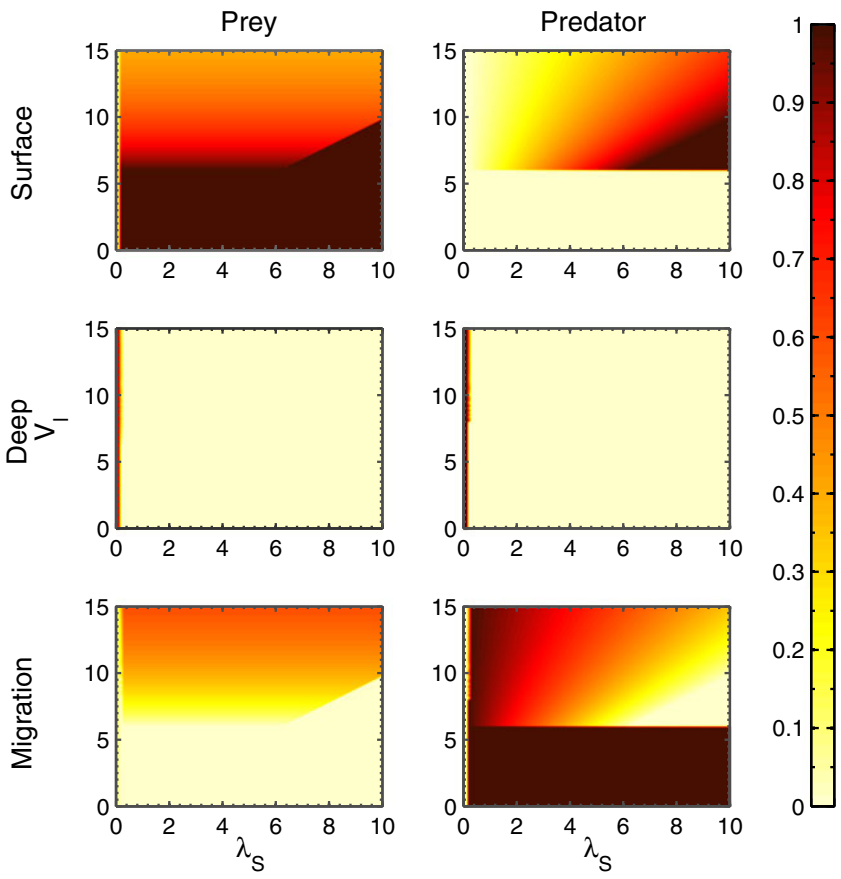

Fig. 3 Distribution of the prey (*left column*) and the predator (*right column*) in the different strategies (surface, deep, and DVM) under the presence of a top predator which forage on the middle predator. On the x-axis, we varied the prey's growth rate in the surface (λ_S), and on the y-axis the intermediate predator foraging voracity in the surface during daylight hour (V_l). The top predator foraging voracity is fixed at $W_l = 6.0$. The *first row* represents the proportion of surface strategy, in the *middle*, the deep strategy, and in the *bottom*, the diel vertical migration strategy while the *top* predator (not represented) is assumed to stay in the surface

versus shallow ones during the night (Bost et al. 2002; Hays 2003). This pattern follows the DVM of the myctophid fish, their main prey, at the Kerguelen islands, throughout the summer (Bost et al. 2002). During their deep dives in daytime, the penguins reduce their time at the surface by 1/3, thus reducing their searching time at shallow waters. It can thus be an advantage for an individual prey to risk staying at the surface, but if the density of prey at the surface becomes too high, the penguins will not perform deep dives any longer as the deep dives are energetically costly due to the necessity to return regularly to the surface to breathe (Hays 2003). At dusk, the penguins' visual performance at the surface layer diminishes and the fish ascend to the surface, inducing shallower dives from the penguins. Although the shallow dives require less energy, the poor rate of prey capture, due to the darkness results in a lower ingestion rate. The prey are therefore safer at the surface at night than in the deep during the day (Hays 2003). The myctophid fish, along with the abundant species of *Protomyctophym*, *Gymnoscopelus*, and *Electrona* are known to perform a DVM in this area (Bost et al. 2002) and are assumed to follow their main prey (copepods, amphipods, and euphausiids) in their vertical pattern (Koz 1995) while avoiding the dangerous surface layers during the daylight hours. Although the myctophid fish can forage all day and night on the copepods, amphipods, and euphausiids, we can assume that those prey, actively feeding in the surface at night, are easier to locate and therefore predate, even in the ambient darkness compared to during their resting mode in deep. A comparable behavior of the penguins had been found in some mesopelagic fish like the big-eye tuna (*Thunnus obesus*) or the swordfish (*Xiphias gladius*) which perform diel vertical migration to track the zooplankton in the deep during the day while performing short excursions to shallower depth to warm up and therefore maintain the advantage of high muscle temperature (Dagorn et al. 2000).

As a second example for the prey and predator performing DVM, we consider the *C. pacificus* copepods in the deep basin Dabob Bay, Washington, USA. *C. pacificus* feed mainly on the phytoplankton and are predated by visual planktivorous fish (Frost 1988; Ohman 1990). We compare the dynamics of the system between 2 years: in April 1979, the concentration of chlorophyll a was relatively low (70 mg chla.m^{-2} in the upper 30 m, Frost 1988), while in April 1985, it

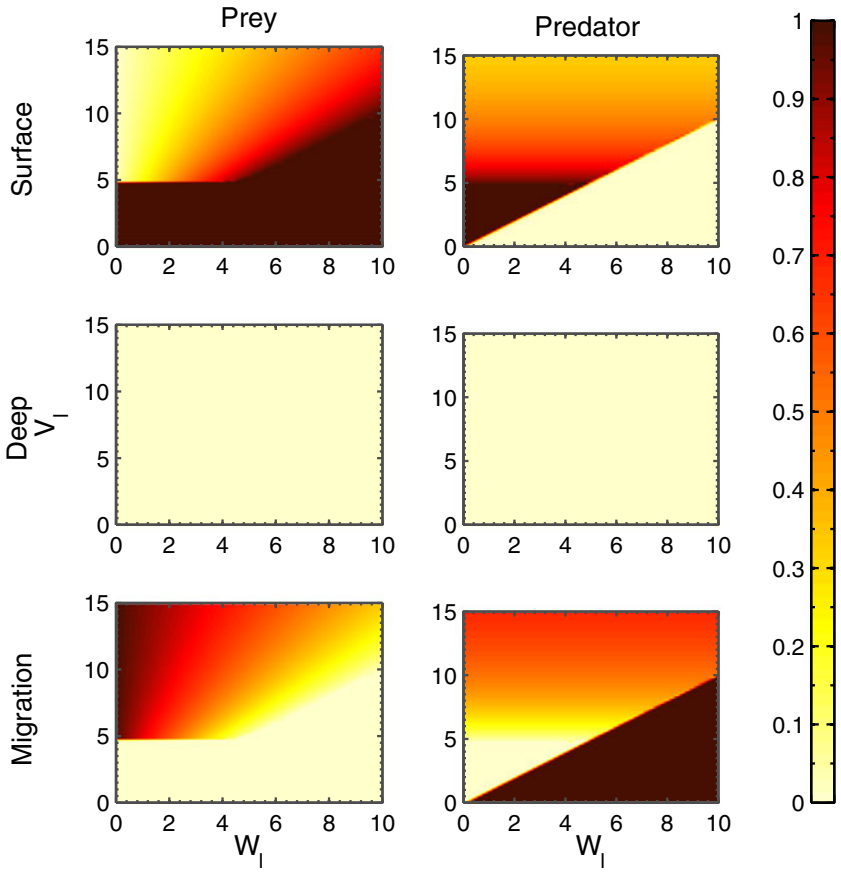

Fig. 4 Distribution of the prey (*left column*) and the predator (*right column*) in the different strategies (surface, deep and DVM) under the presence of a top predator which forage on the middle predator. On the x-axis, we varied the top predator voracity during daylight hour (W_I), and on the y-axis the intermediate predator foraging voracity in the surface during daylight hour (V_I). The prey's growth rate in the surface is fixed at $\lambda_S = 5.0$. The *first row* represents the proportion of surface strategy, in the *middle*, the deep strategy, and in the *bottom*, the diel vertical migration strategy while the *top* predator (not represented) is assumed to stay in the surface

was more than three times higher (250 mg chla.m^{-2}). In presence of low food, the model predicts the prey to migrate even with low predation, while in high food availability (and therefore a potential high growth rate), the prey will choose to stay in the surface unless the predation risk gets very high, which match the observations from Frost (1988).

In the same area, the system consisted by *P. newmani*, the carnivorous copepod *E. elongata*, and a visual planktivorous fish is a good example of the three level interaction: the copepod *E. elongata*'s main prey is the *Pseudocalanus* spp., while they, in turn, are mainly predated on by fish. In July 1979, an high abundance of planktivorous fish (three-spine stickleback *Gasterosteus aculeatus* and the juvenile chum salmon *Onchorhynchus keta*) was observed at one station while the other had a low fish abundance (Ohman 1990). In the presence of the planktivorous fish, the model predicts that the middle predator migrates while the prey takes the opportunity to stay in the surface, matching the observation for the *P. newmani* and *E. elongata* (Ohman 1990). In low level of top predation, the model predicts that the middle predator mainly stays in the surface while the prey will perform a DVM, which conforms to observations (Ohman 1990). Precisely, how this migration pattern may change when prey are exposed to mixed predators (e.g., visual and rheotactic, Visser et al. 2009) remains to be explored, although the basic modeling framework would stay the same.

The fitness measure used in this paper was, it can be argued, the simplest possible choice. First, fitness of an individual is usually measured either as the total reproductive output over the remaining life time (e.g., Hugie and Dill 1994; Visser 2007), or as the specific growth rate of the subpopulation to which the individual belongs (e.g., the present study). See Mylius and Diekmann (1995) for a discussion of the relationship between these two measures. In our case, where we have not posed a complete model of population dynamics, there is no reason to prefer the one or the other except analytical simplicity. For this reason, we have focused on the specific growth rate; initial investigations indicate that our conclusions remain unaltered if we had instead used the reproductive output.

Additionally, our fitness measure has the property that the fitness of an individual is independent of the

strategy played by its conspecifics, if one fixes the strategies of the other species. Stated differently, the specific growth rates show no direct density dependence. This structure was also used by Iwasa (1982), and was criticized in Hugie and Dill (1994) because it does not lead to Nash equilibria which are evolutionarily stable strategies: Once the predators follow the equilibrium strategy, there is no selection for any prey strategy, and vice versa. A symptom of this is that we have to modify the replicator equation (Appendix) for our iteration to always converge to the equilibrium. However, for many real systems, it is plausible that some weak direct density dependence is present, even if it is less tractable to parametrize and quantify this density dependence. If we had included in our model a weak density dependence, then this would stabilize the equilibrium but only shift it marginally. For this reason, in the interest of a minimal model, we have investigated the model without density dependence.

The main assumption behind this model is that prey behave linearly to the amount of food available and to the capacity of the predator to forage them. However, the animal's behavior in nature is influenced by its internal state, as well as environmental factors: on the one hand, it will prefer to risk high predation pressure rather than starve, while a full gut will favor a safer strategy. Thus, individuals can be pushed to deviate form the ideal repartition between habitat (Alonzo 2002) but at a cost of increase competition between conspecific (Flaxman and Reeve 2006). Further, spending time in the deep habitat, either by adopting a deep strategy or a DVM, often results in a reduced growth rate or slower egg development due to a lower ambient temperature. Organisms are often preyed on by different kinds of predators (tactile, visual hunters) and therefore must make a trade-off in their behavior to avoid their most dangerous predators, while still maintaining a high feeding rate. High plasticity in the vertical pattern has been observed in some species of zooplankton as a function of their different predator abundance (Frost and Bollens 1992), thus showing the wide range of responses zooplankton can produce in relation to predation pressure.

Although it was not investigated here, some organisms also perform reverse DVM. This pattern has been observed for small organisms, especially when their main predators use tactile sense and are themselves predated by high-performance visual hunters (Frost and Bollens 1992; Ohman 1990). We also assumed a clear compartmentalization in the food chain. However, predators often forage more than one trophic level distant. The different migration patterns emerging from scenario 2 and 3 and the results from Rosenheim (2004) show the link between trophic relationships and the behaviors they mediated.

Conclusion

Whereas prior investigations of predator–prey interaction using game theory mainly focused in static ways on the predator–prey distribution between two habitats, we show here that DVM between two habitats with different characteristics can be a sustainable strategy under conditions in which predation pressure and food availability are balanced. A game theory approach allows equal consideration of both the predator's and prey's behavior, each pursuing their own goals and responding to environmental conditions and the behavior of conspecific and interspecific players in order to find the best strategy. These considerations reproduce many of the features of DVM observed in nature as well as leading to the emergence of mixed strategies as a possible evolutionary stable state and cascading behavioral effects that project beyond the nearest trophic levels.

Acknowledgements This work was supported by the Greenland Climate Research Centre and the VKR Centre for Ocean Life.

Appendix

Solution scheme

The Nash equilibrium of the game can be found algebraically, by requiring that all strategies which are adopted by a positive fraction of animals share the same fitness, and that all strategies which are not adopted, have no greater fitness. This leads to a set of linear equations. However, this approach is somewhat tedious, because one must treat the boundaries (i.e., solutions where some strategies are not adopted) separately. A more convenient and flexible approach is to use that the Nash equilibrium is necessarily an equilibrium of the replicator equation (see Hofbauer and Sigmund 2003, for background and a precise converse statement).

With this approach, the replicator equation governs the dynamics of the fractions of the different strategies as follows: The fitness of prey (Eq. 2) and of predator (Eq. 3) are used as growth rates of the subpopulations which adopt each strategy. These dynamics do not necessarily mimic real population dynamics, but is merely

a computational method to identify the Nash equilibrium, by marching the replicator equation forward in time until steady state. We formulate the replicator equation in discrete time. In a first step, populations grow according to their fitness:

$$\begin{cases} N'_S(i+1) = N_S(i) + N_S(i)F^+_{N_S}dt \\ N'_D(i+1) = N_D(i) + N_D(i)F^+_{N_D}dt \\ N'_m(i+1) = N_m(i) + N_m(i)F^+_{N_m}dt \end{cases}$$

$$\begin{cases} P'_S(i+1) = P_S(i) + P_S(i)F^+_{P_S}dt \\ P'_D(i+1) = P_D(i) + P_D(i)F^+_{P_D}dt \\ P'_m(i+1) = P_m(i) + P_m(i)F^+_{P_m}dt \end{cases} \quad (8)$$

In the next step, the abundance proportions are renormalized so as to sum to one:

$$\begin{cases} N_S(i+1) = \dfrac{N'_S(i+1)}{N'_S(i+1) + N'_D(i+1) + N'_m(i+1)} \\ N_D(i+1) = \dfrac{N'_D(i+1)}{N'_S(i+1) + N'_D(i+1) + N'_m(i+1)} \\ N_m(i+1) = \dfrac{N'_m(i+1)}{N'_S(i+1) + N'_D(i+1) + N'_m(i+1)} \end{cases}$$

$$\begin{cases} P_S(i+1) = \dfrac{P'_S(i+1)}{P'_S(i+1) + P'_D(i+1) + P'_m(i+1)} \\ P_D(i+1) = \dfrac{P'_D(i+1)}{P'_S(i+1) + P'_D(i+1) + P'_m(i+1)} \\ P_m(i+1) = \dfrac{P'_m(i+1)}{P'_S(i+1) + P'_D(i+1) + P'_m(i+1)} \end{cases} \quad (9)$$

This completes the recursion, which is then iterated until steady state.

Stabilization

The Nash equilibrium is an equilibrium of the replicator dynamics, but not necessarily an asymptotically stable equilibrium. Since our model of fitness does not include a direct dependence of the density of conspecifics, the replicator dynamics may display periodic dynamics which cycle around the Nash equilibrium, similar to the classic Lotka–Volterra system. To stabilize the Nash equilibrium and dampen out these cycles, we modify the replicator equation as follows: We add a proportion "a" of the difference between the last two time steps of the predators proportion in the surface ($P_S(i-1) - P_S(i-2)$), to the proportion of prey in the surface (N_S):

$$N'_S(i+1) = N_S(i) + N_S(i)F^+_{N_S}dt + a(P_S(i) - P_S(i-1)) \quad (10)$$

This computational stabilization mimics damping in physical systems and does not change the system equilibrium value, as at equilibrium, the predator proportion does not change anymore ($P_S(i) = P_S(i-1)$, so $P_S(i) - P_S(i-1) = 0$). Again, we stress that this is merely a computational method for identifying the Nash equilibrium, so an ecological interpretation of this damping term is not necessary.

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Chapter 4

Myopic heuristics versus life-time optimization of daily routines in seasonal environments

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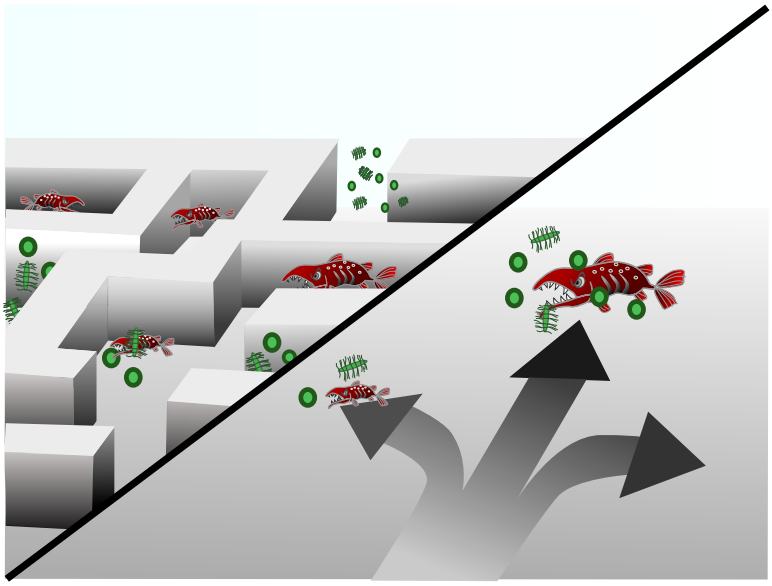

Fig: Analogy of the maze to the dynamic programming where the solution is easily found when the exit is visible against an analogy of patch choice when nothing is available than the current situation.

Myopic heuristics versus life-time optimization of daily routines in seasonal environments

Abstract

Many ecological questions are inevitably determined by behavior, and ecological modelling frameworks which efficiently allow for adaptive and plastic behavioral responses are needed. Life-time behavioral optimization algorithms such as dynamic programming are however, often unsuited for large global models because of their high computational demand. Here, we compare an easily integrated, computationally efficient (analytical) approximation to flexible behavior, against the perfectly optimal behavior solution. The approximation is based on a reduction of the time horizon, taking into account only the current (daily) conditions to optimize behaviour; the so-called "myopic" approximation. We explore the performance of this rule-based approximation with diel vertical migration (DVM) as an example of a daily routine, a behavior with seasonal dependence that trades-off predation risk with foraging opportunities in marine and aquatic environments. When the only behavioral decision pertaining to the optimal solution resides in the migration pattern, the myopic approximation proves to be a robust replacement for the perfectly optimal solution, deviating no more than 25% only in regions of strong seasonality. The myopic approximation has additional advantages in that it can readily accommodate density dependence and inter-annual variations, aspects that can only be accessed in dynamic programming approaches with escalating computational costs. Thus, in ecological models where adaptive DVM behavior is of potential importance, the myopic approximation is in most cases, a robust approach for efficient implementation.

Keywords: diel vertical migration, zooplankton, foraging behavior, habitat selection, latitude, day-length, dynamic programming, myopic, heuristic

4.1 Introduction

Life history strategies emerge from the integrated effects of the moment-to-moment decisions taken by an individual organism over its lifetime. Theses decision schedules or routine (McNamara and Houston 2008, Feró et al. 2008) that best promote the reproductive success of individuals are those that are most likely to be selected for, and should be the most prevalent in natural populations. That is, the optimal decision schedule can be defined in terms of a payoff value. Optimality of the decision schedule can be expected to be strongly dependent on time varying aspects including the development of the individual through different life stages, as well as variations in the environment such as seasonal and daily cycles of food availability and risk of predation (Varpe 2012). There are some general methods to find the optimal decision schedules in terms of an integrated payoff function; such as genetic algorithms based on a Monte Carlo approach (e.g. Hamblin 2013), and dynamic programming that seeks an optimal path through a complex decision-payoff landscape by piecewise backwards integration (e.g. Mangel and Clark 1988). In the search for maximizing organisms behavior, these two methods should zero in on similar optimal solutions (Huse et al. 1999, Sumida et al. 1990, Joh et al. 2001, Strand et al. 2002).

These calculation schemes, while being specifically designed to find optimal solutions, have one serious draw back they are computationally intensive (Bellman 1957). It may not be a problem to find behavioral choices from dynamic programming in a simple model set up, but it is unsuited to interact with, for instance, ecosystem or biogeochemical models. A case in point that serve to illustrate this problem is diurnal vertical migration (DVM) of zooplankton (Angel and Pugh 2000), which has implications for the structure and function of marine ecosystems (Hays 2003). It is also a behavior playing a role in the oceans biogeochemistry, promoting the vertical transport of particulate matter and dissolved gases (Bianchi et al. 2013). In particular, migrating zooplankton excrete and respire a significant fraction of their daily carbon consumption at depths of 200 m or so, bypassing the particulate detritus flux of the euphotic zone, thus contributing to the biological pump (Kobari et al. 2008). The rationale for DVM can be understood as a trade-off between feeding at the surface and avoiding the attention of visual predators (Zaret and Suffern 1976, Lampert 1989, Aksnes and Giske 1993, Fortier et al. 2001, Sainmont et al. 2013). The payoff of a specific DVM behavior (when, how long and how deep to migrate) may be expected to be a function of latitude, time of year, food availability, predator abundance and the state of the zooplankter (Fiksen and Carlotti 1998, Fiksen and Giske 1995); the optimality of which could only be assessed when placed in the context of a full life history strategy. Thus, to produce an exact optimality model of DVM and its impact on, for instance biogeochemical cycling on a global or ocean basin scale, is simply too intensive to be feasible.

An alternative to the full life-history optimization is to base the decision of habitat choice only on the current internal state (e,g, hunger, size, lipid reserves) and the environment. Such a decision is in contrast to the life-history optimization that integrates future events into their behavior. We refer to a decision that only considers the current state of an organism and the immediate environment, with no relation to past or future, as a "myopic" decision (Hutchinson and Gigerenzer 2005). A myopic behavior has the advantage that it is simple and intuitive to formulate and fast to solve, but we also need to know how good the decision is relative to alternatives. Evolution will favor simple heuristics that are quite robust in yielding behaviors with high success in bringing organisms to produce many offspring. Myopic approximations to behaviors, based only on immediately available informations (e.g. daily), have been shown to perform well in conservation ecology when the problem was small and the time horizon was short (Costello and Polasky 2004, Wilson et al. 2006), or when the environment is relatively stable. In strongly seasonal environments a myopic heuristic may not capture the foraging behavioral repertoire as it is unable to account for motivations such as the need for growth (Conover 2003) before the winter, the annual routines, the seasonal or spatial variability in egg fitness (Varpe et al. 2009; 2007).

Our aim here is to explore when a simple decision rule provides a reasonable approximation to the optimal solutions achieved from a full life-history optimization. This facilitates informed decisions on which algorithms to use for including adaptive DVM behavior in more complex ecosystem models.

4.2 Method

To simply the DVM problem, we consider only two distinct habitats: a surface habitat where food is plentiful, but where visual predators are also efficient (the "arena"), and a deeper and darker habitat without food but with much reduced risk from visual predators (the "refuge"). Our aim is to calculate the fraction of the time an organism should spend in the arena τ and the refuge $1 - \tau$ as a function of the body size and environmental conditions. In the following we introduce two methods to find the τ which maximize fitness and then we explore a specific case of a diurnally migrating zooplankton in a seasonal environment. We consider the state w to be individual weight and to influence the income energy (g) and the mortality (μ). We assume that energy is allocated to growth in juveniles ($\psi(w < w_a) = 0$, with w_a the adult weight) and to reproduction in adult stages ($\psi(w > w_a) = 1$). The parameters and variables are described in table 4.1

4.2.1 Dynamic programming

Dynamic programming operates on the future reproductive output of an individual at time t and state w, $F(t, w)$. The optimal behavior τ can be found by solving the dynamic programming equation (e.g. Houston et al. 1999):

$$\frac{\partial F}{\partial t} + \max_{0 \leq \tau \leq 1} \left[\frac{\partial F}{\partial w}(1 - \psi)g + \psi g - \mu F \right] = 0. \tag{4.1}$$

The maximization in this equation expresses a trade-off between energy acquisition (g) and survival (function of the mortality rate μ). The equation is solved numerically by iteration backwards in time from a boundary condition stating that the future reproductive output at any age is zero: $F(\infty, :) = 0$.

4.2.2 Myopic approximation

The dynamic programming equation (eq. 4.1) can be simplified when the environment is constant (aseasonal): $\dot{g} = \dot{\mu} = 0$. The over-dot is a shorthand cut indicating time derivative. It follows that the fitness function (F^*) will not depend explicitly on time, $\dot{F} = 0$ and equation 4.1 simplifies to:

$$\max_{0 \leq \tau \leq 1} \left[\frac{\partial F^*}{\partial w}(1 - \psi)g(\tau) + \psi g(\tau) - \mu(\tau)F^* \right] = 0 \tag{4.2}$$

Since the mortality $\mu > 0$, and the maximum equals 0, we can divide with the mortality function and take the independent function of τ out of the maximization parenthesis to obtain

$$\left[\frac{\partial F^*}{\partial w}(1 - \psi) + \psi \right] \cdot \max_{\tau} \left[\frac{g(\tau)}{\mu(\tau)} \right] = F^* \tag{4.3}$$

by assuming that $\left[\frac{\partial F^*}{\partial w}(1 - \psi) + \psi \right] \geq 0$.

From equation 4.3 it follows that for both phases of ψ (0 and 1), the optimal fraction of time in the arena is the argument which maximizes the "Gulliam rule" (Gilliam and Fraser 1987):

$$\tau^*(w) = \arg\max_{\tau} \left[\frac{g(w, \tau)}{\mu(w, \tau)} \right]. \tag{4.4}$$

The rule 4.4 may be adopted also in situations where there is no life history argument supporting the optimization, for example in situations where the environment changes. In that case, we refer to the rule 4.4 as the "myopic" strategy. Maximizing the ratio g/μ in essence maximizes an individual's reproductive value based on the assumption that future conditions will be identical to those experienced now. To examine the performance of the myopic approximation in a environment where the future conditions are not constant we turn to a specific example of DVM in a seasonally varying environment.

4.2.3 DVM in a seasonal environment

We consider a zooplankton (copepod) that has to make a decision on how to divide the daylight time between feeding at the surface and finding refuge in a deep and safe habitat. Encountered food $R(t, w)$ (cf. Appendix 4.A) at the surface vary over the year. Mortality risk from predation μ_p is to a large degree influenced by light intensity which vary over the year and over the daily cycle depending on latitude. We assume the surface habitat to be as safe during night-time as the deep habitat is at full daylight. It follows then that the individuals should come at the surface to feed at least during the night. The question which remains is how long time the individuals should reside at the surface during daytime (a schematic representation of the model set up is represented in Figure 1.7).

The state of an individual during its life is characterized by its weight w. Size is used to scale physiological rates of search volume, maximum consumption ($C_{\max}$) and standard metabolism (ξ). We consider that the main predation is from a herring type of predator as modeled by Huse and Fiksen (2010). Herring are abundant in the North Atlantic and are an important visual predator of zooplankton. Fish visual detection range and predation efficiency is affected by ambient light radiance, by prey size and contrast (Aksnes and Utne 1997). Thus, predation at the surface increases with prey body size as prey are more easily detected by the visual predator, while in the deep habitat, predation rate decreases when individuals can swim deeper, i.e. their ability to swim increases with size. The specific parameterization of food availability, day length, physiological rates and predation mortality rely on previously published models described in Appendix 4.A-4.C. Finally, we assume that during the winter zooplankton migrate to the deep habitat to overwinter safely and come out of dormancy when the next spring bloom starts.

Growth and mortality

The assumptions about environment and individual physiology together with the behavioral decision determine available energy and mortality at the surface (g_s and μ_s) and the deep (μ_d).

Available energy is determined by consumption, assimilation efficiency and standard metabolism. We introduce the feeding level ($0 \leqslant f(t, w) \leqslant 1$) to indicate the proportion of food ingested compared to the maximum consumption ($C_{\max}(w)$, cf. Appendix 4.C). It is described by a functional response type II with the available food reduced by the fraction of the time spent at the surface τ_s:

$$f = \frac{\tau_s R}{\tau_s R + C_{\max}} \tag{4.5}$$

Similarly, we introduce f_c the critical feeding level ($0 \leq f_c(w) \leq 1$) as the

minimum ingested food required to cover metabolic costs ($\xi(w)$, cf. Appendix 4.C):

$$f_c = \frac{\xi}{\alpha C_{\max}} \tag{4.6}$$

Available energy at the surface is thus defined as:

$$g_s = \alpha C_{\max}(f(\tau_s = 1) - f_c) \tag{4.7}$$

where α is the assimilation efficiency.

Predation mortality in the two habitats depend on environmental conditions (latitude and time of the year) and body size. We assume that the surface habitat is located close to the phytoplankton layer at a depth of $D_s = 30$ meters while the refuge depth is function of the zooplankton swimming capacity. Considering that zooplankton can swim the equivalent of one body length per second during 2 hours, the depth of the refuge is:

$$D_d = D_s + vL_c(w) \tag{4.8}$$

where the length of the individual is converted from its weight (see appendix 4.D, eq. 4.23, Rey-Rassat et al. 2002). The depth determines predation mortality in the surface and the deep habitats (Fig. 4.1).

The average growth and mortality during a day will be determined by the fraction of time in the two habitats and the fraction of time with daylight τ_{day}. They will feed during the night $1 - \tau_{\text{day}}$ and during the fraction of the daylight when they are at the surface $\tau_s - (1 - \tau_{\text{day}})$, while standard

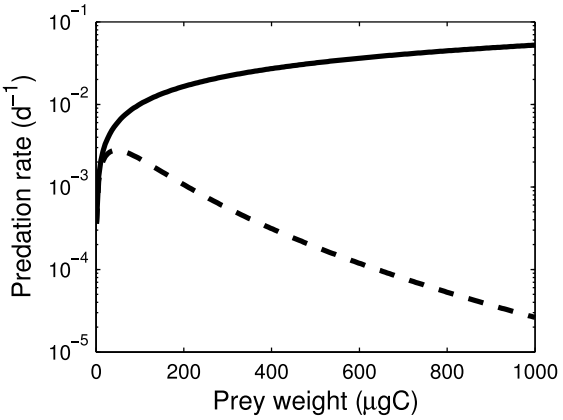

Figure 4.1: Predation rate as a function of the prey weight, at 140 Julian day and a latitude of 70°N at the surface habitat (solid), and the refuge (dashed). The depth of the surface habitat does not change with individual weight, therefore the predation rate increase with the surface area of the prey. In contrast, larger individual can swim deeper, and therefore the refuge become safer with the increase of individual size.

metabolism uses energy irrespective of the habitat. Likewise, will experience surface predation rates (μ_s) while they are located at the surface habitat during daylight hour $\tau_s - (1 - \tau_{\text{day}})$ and reduced predation rate due to darkness (μ_d) during the night $1 - \tau_{\text{day}}$ and in the deep habitat $1 - \tau_s$. The total predation mortality rate is therefore:

$$\mu_p = \mu_s(\tau_s - 1 + \tau_{\text{day}}) + \mu_d(2 - \tau_{\text{day}} - \tau_s) \tag{4.9}$$

and the total available energy and mortality rate μ are thus:

$$g = \alpha C_{\max}(f - f_c) \tag{4.10}$$
$$\mu = \mu_0 + \mu_p \tag{4.11}$$

where μ_0 is a size and time-independent background mortality.

Finally, we assume that individuals will enter diapause to overwinter when the maximum possible growth is negative, i.e. when $f(\tau_s = 1) - f_c < 0$. During diapause individuals migrate to the very deep habitat and reduce standard metabolism by a factor γ. Down there, they are even safer from predation than in the deep habitat (we assume that the predation rate is also reduced by γ: $\mu_p = \mu_d/\gamma$).

Simulation

The simulation with the two methods starts at the beginning of the year, with an individual initial size of w_0 of 100 μgC at the beginning of a year. We follow the development of weight and the future reproductive output through a 10 year simulation, long enough to avoid simulation termination effect on behavior with the individuals following the dynamic programming decision rule. While the dynamic programming problem has to be solved numerically (Appendix 4.E), the myopic approximation (eq. 4.4) admits an analytical solution:

$$\tau_s = \frac{1}{f_{\max}(1 - f_c)} \left(f_c + \sqrt{f_c + f_{\max}(1 - f_c) \left(\frac{\nu}{1 - \nu} - 1 + \tau_{\text{day}} \right)} \right) \tag{4.12}$$

with $\tau_s \in [1 - \tau_{\text{day}}, 1]$ during the spring bloom and 0 in diapause, and $f_{\max} = R/C_{\max}$ is the maximum feeding level possible. The comparability between the two methods is verified in constant (aseasonal) environment, where the two methods should predict the same behavior (see figure 4.F.1, Appendix 4.F).

The lifetime expected reproductive output R_0 is used to compare the two methods. For the dynamic programming $R_0 = F(0, w_0)/w_e$ while for the myopic decision R_0 is calculated as:

$$R_0 = \frac{1}{w_e} \int_0^\infty P(t)\psi(w(t))g(w(t)) \, \mathrm{d}t. \tag{4.13}$$

where the probability to be alive is found by solving $\dot{P} = -\mu(t)P$. There is no density dependence involved in the model.

4.3 Results

We compute the life-time reproductive value for three individuals: one following the optimal dynamic programming method (individual DP), one following the myopic approximation method (individual MA), and a third that does not migrate daily (null strategy; individual H_0). The null strategy serves as a baseline when DVM is not taking into account in the model. We first compare the three individuals in detail in a two-year simulation, where we set latitude to 70°N, and the during of the feeding season to 15 days (figure 4.1). Note how poorly the null strategy individual is doing compared to the other two individuals (panel e), mainly because its survival decreases much faster than the other two individuals (panel c).

Both migration strategies (DP and MA) predict that individuals should come to the surface most of the day at the beginning of the bloom (panel a) in order to maximize their consumption (panel b), and growth (panel d), at the expense of their survival (panel c). The myopic method predicts that individuals should stay all day long, while dynamic programming predicts a short migration to the deep. When the available food increases and consumption approaches its maximum, both individuals reduce the time spent at the surface to night-time duration (gray background, panel a), thereby reducing their feeding potential (the lines are lower than the maximum consumption in dark gray, panel b). Individuals following the three alternative strategies mature at about the same age (pannel d). As individuals obeying H_0 remains at the surface, its feeding level matches the maximum feeding level and its survival is much reduced compared to the migrating individuals.

When the night gets too short to maintain a sufficient feeding level, the migrating individuals risk feeding during part of the daytime. During midnight sun, individuals have to spend more time at the surface to compensate for predation loss by increasing growth. In this situation, individuals with the optimal strategy DP spends a bit more time at the surface than individual MA in order to increase egg production (panel e). When food becomes scarce, individual DP yields a safer strategy than individual MA which maximizes its growth by spending all day feeding at the surface. As a consequence, individual MA ends up with a lower survival but maintain adult size longer than individual DP and thereby partly make up for the lowered survival by a higher reproduction.

During winter, all individuals overwinter and slowly lose weight due to metabolic maintenance. When the bloom starts the following year, individual MA maximizes its growth to regain adult size as fast as possible, while

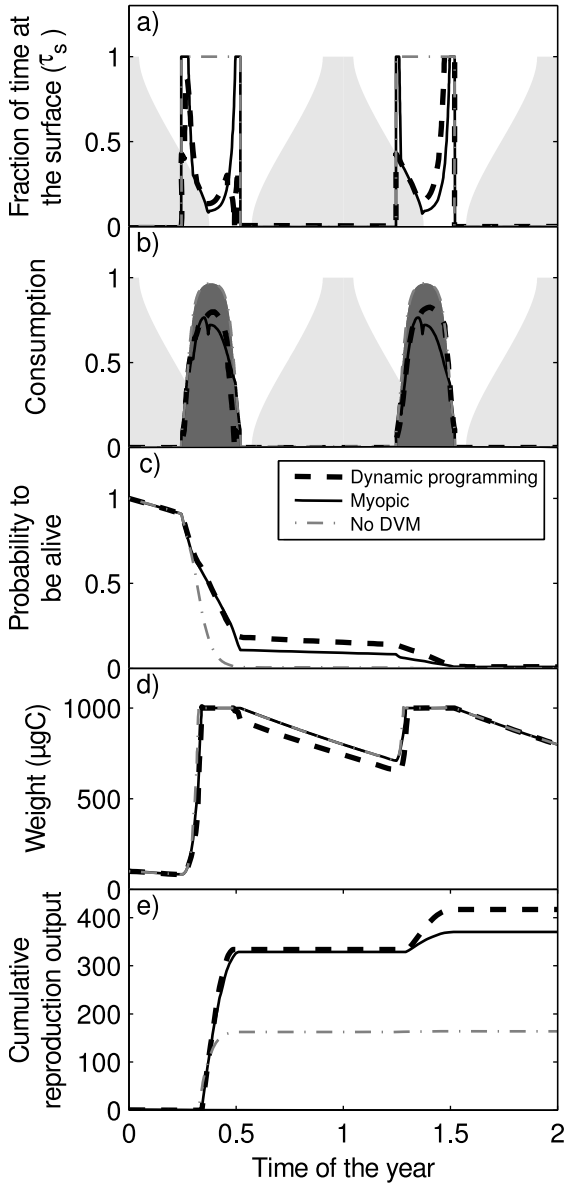

Figure 4.1: Comparison between individuals following dynamic programming (thick dashed line), the myopic approximation (thin black line) and a non-migrating behavior (grey line). The fraction of time the individual spend at the surface with night length represented by the grey patch (a and b) and the maximum feeding level in dark gray background (b). For clarity, we run the model for only 2 years in this case. Weight at the start of the year is 100 μgC, the fish density is 10^{-6} fish m^{-3} and the latitude 70°N.

individual DP plays a safer strategy by returning to the surface to feed only at night. Both migration strategies (DP and MA) predict that individuals should come to the surface to feed only during the night when food is plentiful, but individuals have to increase their feeding when the night gets too short. However, individual MA plays it slightly safer than individual DP. Unlike MA, DP optimizes with the benefit of knowing the future and disregard predation risk to maximize its remaining opportunity for reproduction at the end of the season.

We now investigate a large space range of parameters values to investigate the performance of the myopic approximation relative to dynamic programming. We investigate: latitude, feeding season duration, and mortality, i.e. background mortality and size-dependent mortality described by the density of fish.

4.3.1 Latitude and feeding season duration

In a variable environment, one can expect differences to arise between the dynamic programming and the myopic approximation methods, as individuals following the dynamic programming method optimize their decisions considering their full life time. Mainly, they have knowledge of the duration of the feeding season, and adapt their behavior to this. When looking at the fitness distribution over the latitudinal gradient in seasonal day-length (from the equator to the pole), we see a general decrease in fitness, as individuals have to take more risk to feed when the fraction of daylight hours increases during the summer (i.e. latitude, figure 4.2).

The relationship is slightly more complex when looking at the feeding season duration. In a short bloom, any extra days of feeding increases fitness. However, as we keep the net annual production constant in the system (describing a constant turn over of nutrients, cf. Appendix 4.A), food concentration drops and the peak level decreases as the bloom become longer. When the bloom length becomes long enough, individuals become food limited and they have to spend more time at the surface to gain their daily ration. Furthermore, when the bloom lasts over the summer, the fraction of daylight hours per day decreases at the end of the bloom, and individual can forage longer in low predation risk. Thus an alternation of increasing and decreasing fitness is observed when looking at the feeding season duration gradient, evident for both myopic and dynamic programming decision rules (figure 4.2 a and b).

When comparing the two strategy outputs, the larger differences are found in the short feeding season and at high latitude (figure 4.2 c). However, the decrease value of the ratio in high latitude could be an artifact due to low fitness values, enhancing any existing differences.

Overall, the difference between MA and DP individual fitness is at most 25%, and is only evident in strongly seasonal situations (high latitude with

short feeding season).

4.3.2 Mortality

When increasing background mortality and fish density, individual fitness decreases as expected (figure 4.3 a and b). The highest differences is found when the predation mortality is high, as the myopic method takes usually more risks than predicted by the dynamic programming methods at the beginning of the bloom, which affects life-time fitness. When the fish density is lower than 10^{-6} fish m^{-3}, the myopic approximation explains more than

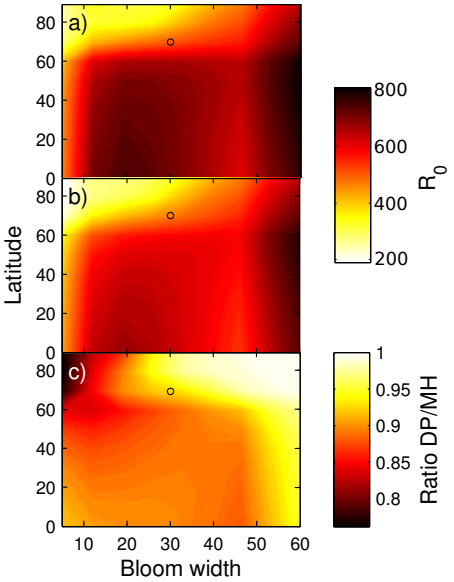

Figure 4.2: Influence of latitude and duration of the feeding season on the fitness of individuals following the dynamic programming (a) and the myopic approximation (b), along with their ratio (c). Running time 10 years, fish density 10^{-6} fish m^{-3}. The open dots indicate the parameters used to compute figure 4.3.

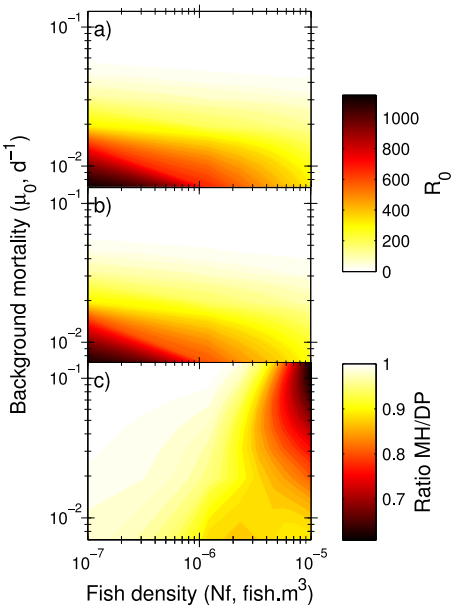

Figure 4.3: Influence of the size independent background mortality (μ_0), and fish density (N_f), affecting the individuals as a function of their size, but also as a function of the environment (latitude, time of the year). We used a latitude of 70°N and a bloom width of 30 days for the calculation. The second x-axis indicates the corresponding predation rate at the surface for an adult individual, during the summer (at 140 julian day). The open dots indicate the parameters used to compute figure 4.2.

90% of the fitness, and can thus easily replace the dynamic programming method. When both the background mortality and the fish density are high, the myopic approximation loses its power, and only explain around 60% of the egg production. This is in any case much higher than the non-migrant strategy which for many cases only explain a small fraction of the possible fitness (figure 4.4).

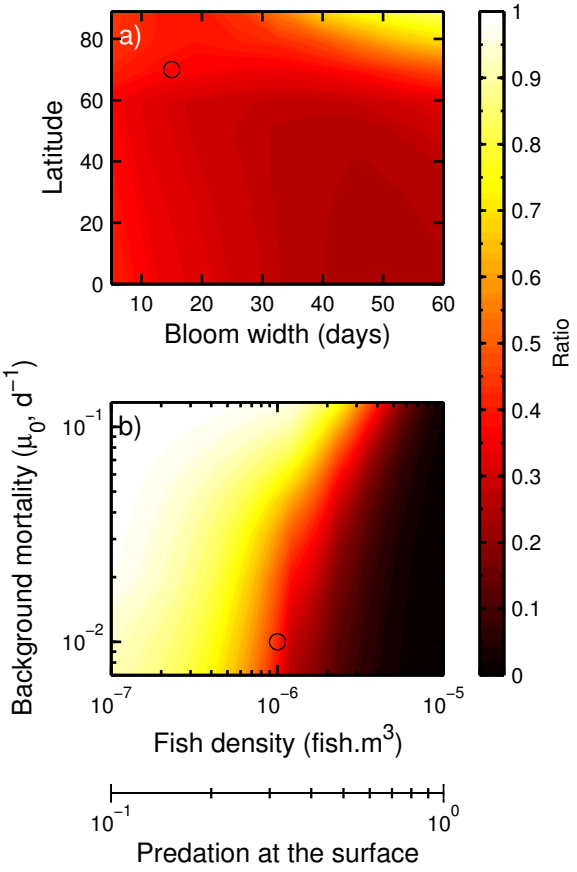

Figure 4.4: Ratio between the non-migrating behaviour and the life time optimization calculated with dynamic programming, for a variation in latitude and bloom duration (a), and over variation of background mortality and density of fish (b). The second x-axis on panel b indicates the corresponding predation rate at the surface for an adult individual, during the summer (at 140 julian day). The circles show the parameters used to compute the other panel: a background mortality of 0.01 d^{-1}, and a fish density of 10^{-6} fish m^{-3} for panel a, and a latitude of 70° with a 30 days of bloom width for panel b.

4.4 Discussion

We have compared two different ways to include DVM in zooplankton models. Under most of the parameter space studied, the myopic approximation method seemed to perform well, with only 10% differences in prediction relative to that of the life-time optimization procedure calculated with dynamic programming. Furthermore, a fitness rate of 0.9 means that the population of DP individuals will be double of the MA's after 6.6 generations. This differences is minimal compared to the internal ecosystem and environmental variability. The simplicity and the low computer power needed by the myopic approximation suggests this to be an efficient alternative to life-time optimization methods as dynamic programming or genetic algorithms. This makes the myopic approximation well suited to be used for describing behavior of higher trophic levels in large circulation models or end-to-end models.

The parameter space region where the myopic method did not show high performance is in high latitudes, short bloom and under high predation pressures, with differences between the two methods raising to 25%. This parameter space corresponds to the polar region, where the high seasonality and high production, strengthen the bloom into a short time of the year, but is still sufficient to sustain a large concentration of fish (Dommasnes et al. 2004), sea birds (Harding et al. 2009, Kampp et al. 2000), jellyfish and ctenophores (Purcell et al. 2010) and, even marine mammals as whales or seals (Laidre et al. 2007, Laws 1977) during the spring bloom (i.e. high predation rate, Thor et al. 2008). In such systems the myopic approximation should be used with care or another methods should be considered.

In every point of the parameter space explored, the myopic method prevailed over a non-migrating strategy without costing computer power (figure 4.4 and Kristiansen et al. 2009). Indeed, even in the region where myopic method was found lacking with respect to dynamic programming (high latitude environments), the non-migration behavior explained only around 40% of the expected reproduction output against 75% with the myopic methods under moderate predation rates. Thus, including DVM is a requirement to capture growth, survival and reproduction of zooplankton in a model. Hence, modelers are facing a choice in front of the need to include behavior in their large ecosystem models. They can hard code a DVM behavior, such as staying at the surface only during night time. However, individuals would starve unrealistically in presence of food availability at high latitude during mid-night sun. Alternatively, they can arbitrarily choose a 50% time foraging, which would induce a reduction of feeding opportunity in early spring. In theses circumstances, a myopic methods such as the one presented in this study is the best alternative to behavior implementation, without increasing computational demands.

The main drawback of optimization procedures is the rigidity of the

framework. White noise in the environment, such as the variation in the probability to find food can easily be implemented in dynamic programming. However, when including randomness in the environment, such as inter-annual variation in the timing of the bloom, the state of the animal must be complemented with environmental state variables to obtain a Markov process which describes the joint dynamics of animal and environment. The number of possible state combinations quickly grows beyond reasonable bounds, which renders computations infeasible. It also raises the question if the animal can be assumed to have perfect information about the future. In inter-annual variable environment the advantage of accounting for the future declines, simply because the future becomes less predictable. Furthermore, density-dependence can not be implemented in a dynamic programming setting. We therefore expect that the myopic approximation improves in these cases.

The importance of DVM was illustrated by a specific model of a zooplankton in a seasonal environment. The specific results are influenced by the assumptions of the model. Regarding mortality, we overestimate the predation rate at the surface as light level used in the daily calculation was at noon, which represent the maximum light intensity of the day. In reality the light level is varying over the day, and the inclination of the sun matters for the light penetration depth. The timing and depth of the phytoplankton bloom was also assumed to be fixed, while it is a function of the thermocline depth, wind pattern, turbidity and of the light attenuation coefficient at the given place and time (e.g. Aksnes and Giske 1993, Sverdrup 1953, Sakshaug et al. 1991, Huisman et al. 1999). The 30 meters depth, was then used as a reference to compute the depth of the refuge habitat and thus entered in the calculation of the surface and deep predation mortality rate. We also assumed that the zooplankton had no food available in the deep, while they can partially feed on marine snow or detritus as an alternative to the rich phytoplankton bloom (Hansen et al. 1996, Alldredge and Silver 1988), and that there is no influence of the bloom on light attenuation. Nevertheless, we expect that the general results about the importance of resolving DVM (e.g. Pearre 2003; and present study) and the relative merit of the myopic approximation are unaffected by the assumptions of the zooplankton model.

In our calculation of the expected reproduction output fitness measure, we assume that all the eggs have the same fitness value, independent of the time of year they are born. However, modeling studies have shown that eggs spawned prior to and at the beginning of the season have a much higher fitness compared to the offspring born at the end of the feeding season (Varpe et al. 2007). Similarly, capital breeding has been shown to be a successful strategy, especially in short feeding seasons (Sainmont et al. ted a), thus leading individuals to store reserves to be able to spawn before the feeding season. These capital breeding individuals are highly vulnerable to visual predators, due to their large size and fulled storages while they still

have not yet reproduced (Hays et al. 2001, Sainmont et al. ted b). In this circumstances, individuals could favors their survivorship over any feeding opportunities, changing thus the growth over mortality fitness optimization used with the myopic approximation. We could thus expect these individuals to favor deep distribution over any kind of migration. The change of priority over the life time can emerge in dynamic programming optimization but are lacking in the myopic approximation.

Conclusion

We have shown that resolving behavior is crucial for the lifetime reproductive output of higher trophic levels. The myopic approximation is a viable alternative to full life time optimization method as dynamic programming, when the environmental conditions are not too harsh, i.e. not in high latitude, short bloom or under high predation mortality. It can be used in regional or global bio-geochemical models where the focus is not on optimal behavior nor individual state and when computational time is an issue. The myopic heuristic is also useful when modeling inter-annual variation in the timing of the bloom or in density dependent situations where techniques like dynamic programming are difficult to implement.

Acknowledgements

This work was supported by the Greenland Climate Research Centre and the Centre for Ocean Life, a VKR center of excellence supported by the Villum foundation.

Table 4.1: List of symbols and parameters. The units used are liters (L), microgram carbon (μgC), meter (m), individuals (ind), second (s) and days (d).

Symbols	Descriptions	Values	Units
F	Future reproductive output		biomass
R_0	Lifetime expected reproduction output		number of eggs
R	Encountered food		μgC d^{-1}
w	Weight		μgC
P	Probability to be alive		
t	Time		d
ξ	Standard metabolism		μgCd^{-1}
g	Available energy		μgCd^{-1}
g_s	Available energy at the surface		μgCd^{-1}
μ	Mortality rate		d^{-1}
μ_p	Total predation mortality rate		d^{-1}
μ_s	Predation mortality rate in the surface habitat		d^{-1}
μ_d	Predation mortality rate in the deep habitat		d^{-1}
ν	Ratio surface/deep predation mortality	μ_d/μ_s	
N_f	Density of fish		fish m^{-3}
$C_{\max}$	Maximum consumption rate		μgC d^{-1}
f	Feeding level	[0,1]	
f_c	Critical feeding level	[0,1]	
$f_{\max}$	Maximum possible feeding level	[0,1]	
τ_{day}	Fraction of daylight per day	[0,1]	
τ_s	Fraction of time at the surface	[0,1]	
L_c	Individual length		μm
ϕ	Latitude		°
D_d	Depth of the deep habitat (individual size dependent)		m
V_s	Clearance rate		L d^{-1}
Parameters			
w_e	Egg weight	1	μgC
w_a	Adult weight	1000	μgC
γ	Factor of reduction in critical feeding level and predation mortality during diapause	10	
D_s	Depth of the surface habitat	30	m
v	Swimming speed coefficient	7200	s
α	Assimilation efficiency	0.6	
ψ	Fraction of available energy allocated to reproduction	$0, 1$	

Appendix

4.A Food availability

The phytoplankton bloom is modeled as a gaussian function centered around the time T_p, with a width σ and amplitude $a = 80000$ μgC d^{-1}. The food concentration is multiplied by the clearance rate of an individual to arrive at the encountered food (function of the time of the year t, and the individual weight w):

$$R(t, w) = V_s \frac{a}{\sigma\sqrt{\pi}} \exp\left(\frac{-(t - T_p)^2}{2\sigma^2}\right). \qquad \mu\text{gC} \cdot \text{L}^{-1} \tag{4.14}$$

Where the amplitude (a) is equal to 80000 μgC d^{-1}, and V_s is the clearance rate (weight dependent, cf. Appendix 4.C). In moderate and high latitude, the phytoplankton bloom duration is in the order of weeks, leaving zooplankton without food the rest of the year.

4.B Daylight cycle

Use the model by Forsythe et al. (1995). If t is the time of the year (in day), and ϕ the latitude, then τ_{day} is the daylength.

$$\begin{cases} P = \arcsin\left(\beta_1 \cos\left(\beta_2 + 2\arctan\left(\beta_3 \tan\left(\delta(t - \theta)\right)\right)\right)\right) \\ \tau_{\text{day}}(t_y, L) = 1 - \dfrac{1}{\pi} \arccos\left(\beta_4 + \sin\left(\dfrac{\pi \frac{\phi}{\varphi} \sin(P)}{\cos\left(\pi \frac{\phi}{\varphi} \cos(P)\right)}\right)\right) \end{cases} \tag{4.15}$$

with ϕ the latitude, $\beta_1 = 0.39795$, $\beta_2 = 0.2163108$, $\beta_3 = 0.9671396$, $\beta_4 = 0.0145$, $\delta = 0.00860$ d^{-1}, $\theta = 186$ d and $\varphi = 180°$.

4.C Individual conditions

The standard metabolism cost (ξ), the maximum consumption (C_{max}) and the search volume (V_s) are all a function of the individual weight (Levinsen et al. 2000, Saiz and Calbet 2007).

$$\xi = k_\xi w^{3/4} \qquad \mu\text{gC d}^{-1} \tag{4.16}$$

$$V_s = k_v w^{0.7} \qquad \text{L d}^{-1} \tag{4.17}$$

$$C_{\max} = k_c w^{0.7} \qquad \mu\text{gC d}^{-1} \tag{4.18}$$

with $k_\xi = 0.07$ μgC$^{1/4}$ d^{-1}, $k_v = 15.810^{-3}$ μgC$^{-0.7}$ L d^{-1} , and $k_c = 1.68$ μgC$^{0.3}$ d^{-1}.

4.D Visual predation

Fish predation efficiency is affected by the light condition (brightness, contract of the water), by its visual detection range and by prey size. We use the predation model developed by Huse and Fiksen (2010), assuming an herring type of predators. Herrings are abundant in the North Atlantic and is an important visual predators of zooplankton. Predation rate function of the prey weight (w, figure 4.1). Predation rate follows the Holling type II functional response:.

$$\mu_f(t, D, \phi, w) = \varrho \frac{C_f N_f}{1 + C_f h N_f} \qquad \text{d}^{-1} \tag{4.19}$$

with ϱ the conversion factor from second to day ($\varrho = 86400$ d s^{-1}). The predation at the surface habitat is hence $\mu_s(t, \phi) = \mu_f(t, D_s, \phi)$, and in the deep habitat $\mu_d(t, \phi) = \mu_f(t, D_d, \phi)$.

$$C_f = \pi R_f^2 v_f \qquad \text{m}^{-3}\ \text{s}^{-1} \tag{4.20}$$

and where R_f, the visual detection range, can be approximated by:

$$R_f \approx \sqrt{C_{cf} A_c(w) E \frac{I(t, D, \phi)}{k_e + I(t, D, \phi)}} \qquad \text{m} \tag{4.21}$$

when $R_f < 0.05$.

The predation rate μ_f is expressed in d^{-1}, with C_f the clearance rate of the fish, N_f the density of fish (fish m^{-3}), h the handling time (1 s^{-1}), v_f the fish velocity (2 body length per second - m s^{-1}), C_{cf} the contract (0.3, Utne-Palm 2005), K_e is equal to 5 μmol photon s^{-1} m^{-2} (Aksnes and Utne 1997). $I(t, D, \phi)$ is the irradiance at a given time of the year, latitude and depth (eq. 4.22), and function of the irradiance at the surface at the given time and latitude (I_0, Brock 1981), the diffuse attenuation coefficient (k=0.1 m^{-1}, Huse and Fiksen 2010), and depth (D).

$$I(t, D, \phi) = I_0(t, \phi) \exp(-kD) \qquad \mu\text{mol photon s}^{-1}\ \text{m}^{-2} \tag{4.22}$$

The image area of the copepods A_c is a function of the individual weight, assuming a conversion from weight to length (eq. 4.23, Rey-Rassat et al. 2002) and that copepods width is 3 times smaller than its length, and correcting

the rectangular shape with a factor of 0.75 (eq. 4.24, Fiksen and Folkvord 1999).

$$L_c(w) = 3.95w^{0.36} \qquad \mu\text{m} \tag{4.23}$$

$$A_c(w) = 0.75\frac{L_c^2}{3} \qquad \mu\text{m}^2 \tag{4.24}$$

4.E Dynamic programming numerics

Dynamic programming finds the optimal individual behavior as a function of individual's weight and time of the year. The optimal time individuals should spend at the surface is calculated backward starting from the end of the year with a null fitness for individual lower than the maturity size, and a fitness proportional to their weight when higher. Time and individual weight are discretized, and we ensure that the optimization is made within a discrete weight cell ($g\partial t < \partial w$). At each time step, the optimal fraction of time individual should spend at the surface is calculated for all the individual weight classes. At the end, we obtain a matrix of the best individual behavior as a function of their weight and the time of the year, which correspond to the best patch individuals should choose to balance mortality and growth in order to optimize their expected lifetime reproduction output within the set time horizon.

Before maturation ($w < w_a$)
F being the fitness measure, g the growth rate (eq. 4.7), and μ the predation mortality rate (eq. 4.11), for each time step, we find τ_s the optimal fraction of time individual should spend at the surface to maximize the fitness equation (e.g. Mangel and Clark 1988):

$$\frac{\partial F}{\partial t} + \max_{\tau_s}\left[\frac{\partial F}{\partial w}g - \mu F\right] = 0 \tag{4.25}$$

by dividing by F, and by passing in the log scale we have:

$$\frac{\partial \log F}{\partial t} + \max_{\tau_s}\left[\frac{\partial \log F}{\partial w}g - \mu\right] = 0 \tag{4.26}$$

At any state w_i, the present time is calculated relying on the forward time information:

$$\log F(t, w_i) = \log F(t+1, w_i) + \max_{\tau_s}\left[\frac{\partial \log F}{\partial w}g - \mu\right]\partial t \tag{4.27}$$

with $\dfrac{\partial \log F}{\partial w} = \dfrac{logF(w_{i+1}, t+1) - logF(w_i, t+1)}{w_{i+1} - w_i}$.

The optimal τ_s^*, solution to the equation 4.26 is:

$$\tau_s = C_{\max}\left(-\frac{1}{V_s R} + \sqrt{\frac{\frac{\partial \log F}{\partial w}\alpha}{\mu_s(1-\nu)V_s R}}\right) \tag{4.28}$$

Spawning ($w > w_a$)
Once the individuals reach maturity, they stop growing, and allocate the energy surplus to reproduction. The fitness function can then be written as:

$$\frac{\partial F}{\partial t} + \max_{\tau_s}\left[g - \mu F\right] = 0 \tag{4.29}$$

Here g is no longer the growth rate but the energy accumulation allocated to reproduction (eq. 4.7 still apply). Dividing by F, we have:

$$\frac{\partial \log F}{\partial t} + \max_{\tau_s}\left[\frac{g}{F} - \mu\right] = 0 \tag{4.30}$$

The fitness at present time is thus calculated for each individual weight w_i as a function of the state at the forward time:

$$\log F(t, w_i) = \log F(t+1, w_i) + \max_{\tau_s}\left[\frac{g}{F(t+1, w_i)} - \mu\right]\partial t \tag{4.31}$$

The optimal τ_s^* is therefore found by:

$$\tau_s = C_{\max}\left(-\frac{1}{V_s R} + \sqrt{\frac{\alpha}{\mu_s(1-\nu)V_s R F}}\right) \tag{4.32}$$

4.F Constant environment

A simple verification on the well founded of the myopic method can be done in constant (fixed) environment. Indeed, in a fixed environment (i.e. the light regime and food abundance is constant), the myopic method should predict the same strategy (i.e. the same fraction of time at the surface τ_s). We test the similitude of the two optimization methods for different time of the year over a range of state (i.e. individual weight, figure 4.F.1).

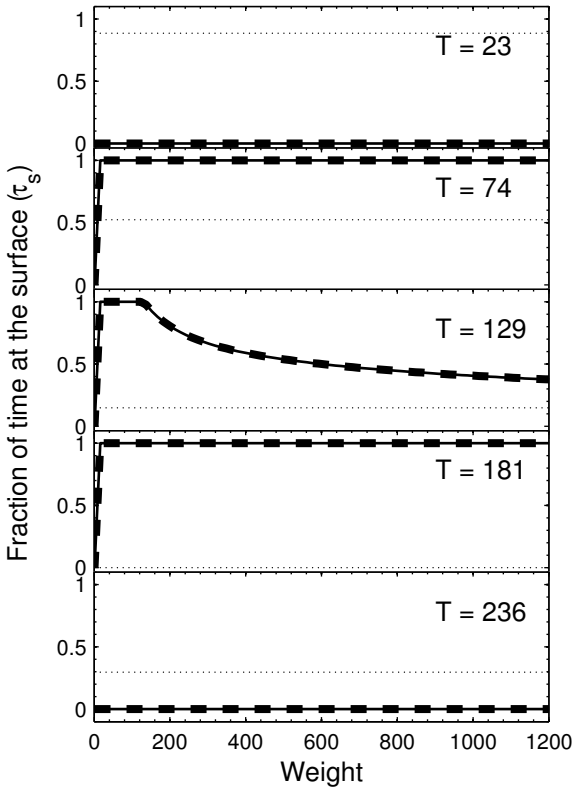

Figure 4.F.1: Fraction of time individual should spend at the surface simulated with dynamic programming (bold dashed line), and with the myopic methods (thin line) represented at given time of the year for the range of individual weight. The thin dotted lines represent the fraction of night-time per day.

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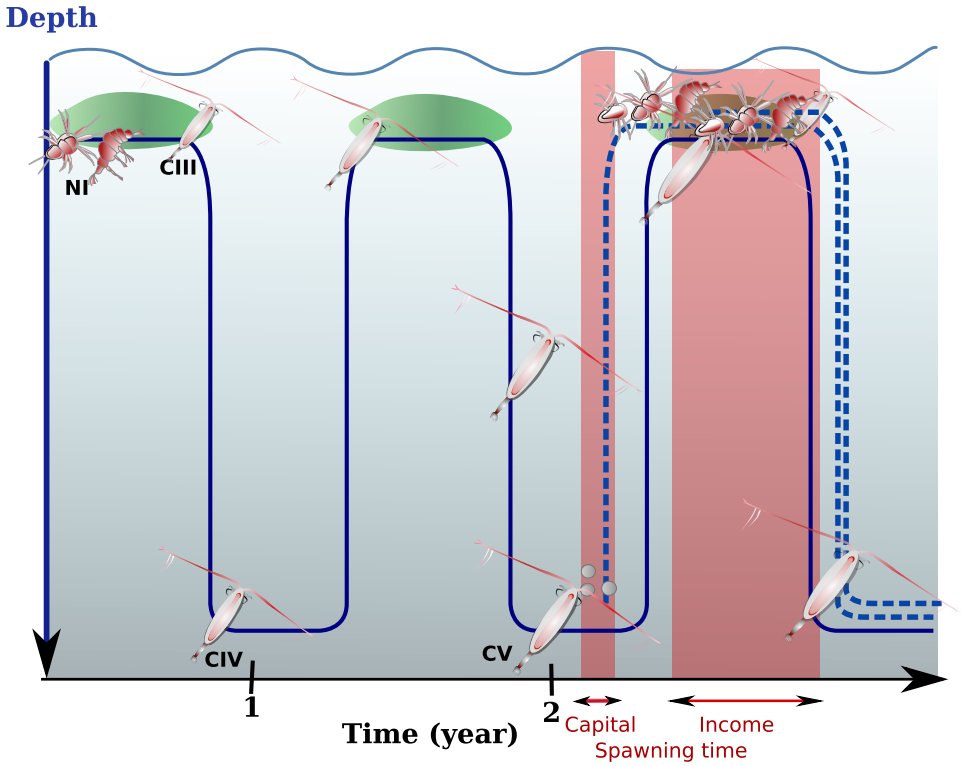
Part II

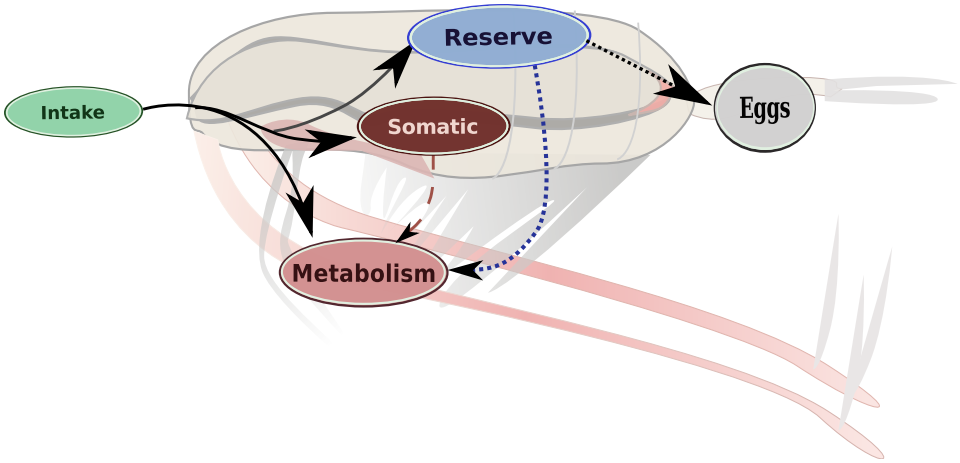
Resource allocation to reproduction: income versus capital breeding


Depth
NI
CIII
CIV
CV
1
2
Time (year)
Capital
Income
Spawning time

Chapter 5

Income versus capital spawning at high latitudes: modelling copepod reproductive strategies

Sainmont, J., Andersen, K. H., Varpe, Ø, and Visser, A. W.



Income versus capital spawning at high latitudes: modelling copepod reproductive strategies

Abstract

In high latitude environment, copepods have developed a range of reproduction strategies to cope with the strong seasonality. Some species rely on the incoming food resource to induce reproduction (income breeders), while others use the previously stored reserves to spawn during the winter in total absence of food availability (capital breeders). We use an individual based model to approach the question of pay off between income versus capital breeders and size at maturity in a highly seasonal environment, and therefore look at the potential switch in the zooplankton community composition under climate change. Big capital breeders performs better when the spring bloom is short and intense while they are out-competed by the small income breeder in longer spring bloom. Those results are in agreement with the distribution of the copepods *Calanus finmarchicus* and *Calanus hyperboreus* in the North Atlantic and in the Arctic oceans.

Keywords: Income, Capital, spawner, breeder, *Calanus finmarchicus*, *Calanus hyperboreus*

5.1 Introduction

The dichotomy between income versus capital breeders is a common choice in the life strategies adopted by organisms living in seasonally modulated environments. It has been studied mainly in terrestrial animals (snakes Lourdais et al. 2002, ants Johnson 2006, deer Andersen et al. 2000) but also in birds (penguins Meijer and Drent 1999, migrating birds Broussard et al. 2005) and in marine mammals (seals, Houston et al. 2007, Boyd 2000). Income breeding is often the best option in predictable environments with regular and plentiful food resources (Jönsson 1997). It is, however rarely the case in nature, when food undergoes strong seasonal fluctuations. Relaying on stored energy, capital breeders have the freedom to produce their offspring at times which favor their growth and survival (Varpe et al. 2009), and can be a competitive strategy in variable or modulated environments. Nevertheless the parents have to support the cost of carrying the extra reserves while taking the risk of being killed before having the chance to reproduce (Jönsson 1997, Bonnet et al. 1998). This carrying cost is variable among species. For example, many ectotherms animals are predisposed to carry reserves, which lead to a preference for capital breeding (Bonnet et al. 1998), while many birds have a high cost of carrying extra reserves as it decreases their capacity of movement and therefore increases their risk of predation. Their poor capacity of storage induces the reproduction to be based in some degree on income breeding (Bonnet et al. 1998).

In the Arctic, the environment is highly seasonal, alternating between long, dark winters with no primary production to a short but intense bloom in the spring, and suppressed summer primary productivity (Sakshaug 1997, Falk-Petersen et al. 2007). The timing and duration of the spring bloom, which essentially fuels the entire annual production cycle, is strongly related to local environment as well as latitude, from early and long in the open water of the North Atlantic to late and short in the high Arctic ocean, correlated with the ice break-up (Gosselin et al. 1997, Falk-Petersen et al. 2007, Leu et al. 2011).

Copepods, living in these high latitude environments, display common behaviors in order to avoid their predators and cope with the seasonal environment. They perform diel vertical migration (DVM) during the feeding season, allowing them to feed on the phytoplankton at the surface during the night, and escape the visual predator by finding refuge in deeper, darker layers during the day (Zaret and Suffern 1976). This vertical daily movement is common among zooplankton and small fish species across a wide range of environments, and constitutes perhaps the largest biomass movement on earth (Hays 2003, Angel and Pugh 2000). DVM is strongly correlated with the day-length and predation risk, but also with the need to acquire energy/carbon to cover metabolic costs, to reproduce and potentially, to gather storage reserves before the winter. Copepods also perform

an important annual migration to find refuge in the very deep layer of the ocean during the winter and enter a diapause stage which allow them to greatly reduce their metabolic cost. Indeed it is also a way to avoid predators during the winter when their reserves allow them to dive at great depth (Visser and Jónasdóttir 1999).

In this work we present an idealized model of the life cycle of a generic copepod to explore the mechanisms and costs versus benefits inherent in income-capital breeding life strategy trade-off. We use an individual based model, following the weight dynamics to explore the common life history strategy of two income and two capital breeders with each a small and a large size at maturity. Our goal is to relate the best size at maturity and pure reproduction strategy to the length of the spring bloom.

The weight of *Calanus finmarchicus* and *Calanus hyperboreus* are taken as references for our small and large maturity size strategies. Theses two copepods are present in the North Atlantic and the Arctic environment and displaying different reproduction strategies: *C. finmarchicus* spawns only during the spring bloom, relaying on the incoming food to mature their eggs while *C. hyperboreus* spawn in the deep during the winter, relaying only on reserves accumulated the previous spring bloom. They, therefore, behave closely to income and capital breeders respectively, and will be used for reference in this study.

We use an individual based model to compare the reproduction and size at maturity strategies. Cohorts are differentiated by the individual date of birth with a five-day resolution. The probability to be alive as well as the weight dynamic evolve with time, as a function of the environment forcing. We look at the population growth rate without any density dependence, assuming that the spring bloom is not depleted by the secondary production but by the lack of nutrients. As we keep the amount of nutrient constant in the system we investigate only each strategy fitness (i.e. small income, large income, small capital and large capital breeders) relative to the bloom duration. We also take DVM into account based on a myopic approach.

5.2 Methods

The model is based on the weight of individuals, and its dynamics through the full life history of a copepod as it changes with ingestion, growth, storage, reproduction and starvation. The model investigates the life-time fitness outcome of different reproduction strategies (income-capital breeding, spawning time, weight at maturity) as played out against the environmental setting of the timing and duration of the spring bloom, and seasonal variation of day-length. The organism's weight is divided into somatic (W_s) and reserve weight (W_r). We assume that the individuals can only store reserves once its somatic pool is completed (i.e. reached maturity size) and

that reserve alone can contribute to egg production. Copepods go through 6 stages of Nauplii and 5 copepodites stages before molting to adults, however we do not take these stages into account in this study. Instead, we assume a non-feeding stage (i.e. from egg to Nauplii II stage), an intermediate (i.e. $W_s < W_a$) and a mature individual (i.e. $W_s = W_a$) which is able to store reserves and reproduce.

DVM is included in the model with a myopic approach, meaning that only the current state of the individual and current environmental conditions are considered for this behaviour. The fraction of time spent foraging at the surface is optimized as the ratio between growth and predation mortality rates (Gilliam's rule, Gilliam and Fraser 1987). Hence, we combined short term behaviour (i.e. DVM) with life-history strategies (i.e. breeding strategy; such as suggested in Fiksen 1997). The main strength of this optimization is the robustness during mid-night sun: copepods will still come to eat at the surface but will stay a minimum of time (cf. Appendix 5.A; compared to model such as Sainmont et al. 2013).

Although the foraging, the standard metabolism and the mortality are function of the individual weight, the use of reserves to reproduction differs among breeding strategies: income breeders is assumed to allocate reserves directly to eggs production while capital breeders spawn once a year.

Through the method section, we display the units after each equations. The parameters and variables are resumed in table 5.1.

5.2.1 Food dynamics

The spring bloom, characterized by its width (w), is centered around the time (T_p), while the amplitude is linked to the width ($a/(w\sqrt{\pi})$) to keep the amount of nutrient constant in the system (i.e. the integral of the function is constant, when varing w). The bloom dynamic is computed relative to the time of the year (t, in days) by the function R(t):

$$R(t) = \frac{a}{w\sqrt{\pi}} \exp\left(\frac{-(t - T_p)^2}{2w^2}\right) \qquad \mu\text{gC}\cdot\text{L}^{-1} \tag{5.1}$$

5.2.2 Somatic and reserve weights dynamics

Copepod food consumption is a function of food availability R(t) and their ability to ingest food (maximum consumption C_m - inverse of the handling time) which follow the Holling functional responses type II:

$$C(t) = \frac{V_s R(t)}{1 + \frac{V_s}{C_m} R(t)} \qquad \mu\text{gC} \cdot \text{d}^{-1} \tag{5.2}$$

where the search volume V_s (volume of water explored by the copepods per day) and the maximum consumption C_m are function of body mass at the

power 0.7:

$$V_s = k_v W_s^{0.7} \qquad \text{L}\cdot\text{d}^{-1} \tag{5.3}$$

and

$$C_m = k_c W_s^{0.7} \qquad \mu\text{gC}\cdot\ \text{d}^{-1} \tag{5.4}$$

W_s, the somatic weight is expressed in μgC (Levinsen et al. 2000, Saiz and Calbet 2007). The copepod gain a proportion α (assimilation efficiency) of the ingested food.

Similarly, the standard metabolism is considered to be related to the individual weight:

$$\xi = k_s W_s^{\frac{3}{4}} \qquad \mu\text{gC}\cdot\text{d}^{-1} \tag{5.5}$$

Foraging behavior

At high latitude, DVM is a common feature in the zooplankton community: individuals stay safe in the deep during the brighter hours, and come at the surface when the intensity of light is reduced. During midnight sun, copepods still perform DVM to satisfy their feeding need, at a smaller risk when the intensity of light decreases. The proportion of daylight hour per day τ_D is found relatively to the latitude and the time of the year (model from Forsythe et al. 1995).

To take into account the reduced foraging time and mortality in function of the latitude and the time of the year, we look at the optimal fraction of time copepods should spend at the surface (τ_s) to maximize their short term fitness in function of the consumption, the time of the year and the mortality at the surface and in the deep (cf. Appendix 5.A)

Resource allocation

Copepods allocate food intake in priority to cover the metabolic needs. Depending on the stage of the individuals, the surplus of energy ($\alpha C - \xi$) is allocated to growth [for juvenile] into somatic weight (W_s), or reserves [adult] into the reserve pool (W_r). In case of food deprivation, the standard metabolic cost will be covered by the internal reserves (W_r) of the individual. However, if the reserves are empty ($W_r = 0$), the animals will dig into the somatic weight but will suffer from starvation mortality (m_s, cf. section 5.2.4).

The egg and the first two stages of Nauplii do not feed, therefore the metabolic cost rely on the internal reserves given at birth, during the time needed to develop from egg to Nauplii III. We also take into account the reduction of standard metabolism during diapause (overwintering stage of copepods). We assume that they find refuge at great depth when the maximum surplus of energy they can reach at the surface ($\alpha C - \xi$) is inferior to

the reduced metabolic cost in a diapause stage ($\xi/10$). The energy gain is therefore:

$$G = \begin{cases} -\xi & \text{for age} < \text{Development time from eggs to NIII} \\ \alpha C(t) - \xi & \text{for } \alpha C(t) - \xi > -\xi/10 \\ -\xi/10 & \text{for } \alpha C(t) - \xi < -\xi/10 \end{cases} \tag{5.6}$$

Thus, the somatic weight dynamics can be resumed by:

$$\frac{\partial W_s}{\partial t} = \begin{cases} G & \text{for } (W_s \leq W_a \text{ or if } (W_s > W_a \text{ and } W_r(t) + \alpha C(t) - \xi < 0)) \\ 0 & \text{for } W_s > W_a \text{ and if } W_r(t) + \alpha C(t) - \xi > 0 \end{cases} \tag{5.7}$$

and the reserves by:

$$\frac{\partial W_r}{\partial t} = \begin{cases} G & \text{for } W_s \geq W_a \text{ and } W_r(t) + \alpha C(t) - \xi \geq 0 \\ 0 & \text{otherwise} \end{cases} \tag{5.8}$$

5.2.3 Reproduction

Depending of the species, the spawning process differs: the income breeder spawn during the spring bloom, once they reach the adult stage, while the capital breeder store all the surplus of energy into the reserve pool, and spawn once a year. We assume in this model that the reproduction is only based on the reserve weight.

We assume that the income breeder will spawn whenever the individuals have enough reserves to produce 50 eggs:

$$\begin{cases} N_e(t) = W_r(t)/W_e & \text{for } W_r(t)/W_e > 50 \\ N_e(t) = 0 & \text{otherwise} \end{cases} \tag{5.9}$$

while the spawning happened only once a year for the capital breeders converting the entire reserve to eggs production.

$$\begin{cases} N_e(t) = W_r(t)/W_e & \text{for t = Spawning time} \\ N_e(t) = 0 & \text{otherwise} \end{cases} \tag{5.10}$$

where W_e is the egg somatic weight.

5.2.4 Mortality

The mortality m_T is composed of: 1) a predation mortality m_p function of the total copepod weight ($W = W_s + W_r$) and the time of year t, 2) a starvation mortality, m_s and, 3) a background mortality, m_0. This background mortality assures that the copepods still suffer from some mortality during the winter, in abscence of light and account for natural mortality.

$$m_T = m_p(W, t) + m_s + m_0 \tag{5.11}$$

The predation mortality m_p is function of the individual weight (W; Peterson and Wroblewski 1984, Hirst and Kiørboe 2002, Brown et al. 2004, Andersen and Beyer 2006) and the fraction of time spend foraging at the surface (τ_s) at the surface relative to the fraction of daylight hour per day (τ_D).

$$m_p(W,t) = \begin{cases} cW^{-1/4}[\tau_s - 1 + \tau_D + (2 - \tau_s - \tau_D)\nu] & \text{for } \tau_s > 1 - \tau_D \\ cW^{-1/4}\nu & \text{otherwise} \end{cases} \tag{5.12}$$

where c is a constant and ν is the reduction of predation mortality in the deep (refuge) compared to the surface.

The starvation mortality is applied when the energy income of the copepod and reserves are not sufficient to cover metabolic costs.

$$m_s = \begin{cases} 0 & \text{for } G > 0 \text{ or for } W_r + G < 0 \\ k_m \dfrac{G}{W_s} & \text{otherwise} \end{cases} \tag{5.13}$$

Table 5.1: List of symbols used. The units used are liters (L), microgram carbon (μgC) and days (d).

	Description	Values	Units	References
Variables				
R	Amount of resources		μgC.L^{-1}	
W_s	Somatic weight		μgC	
W_r	Reserve weight		μgC	
P	Probability to be alive			
N	Number of individual in a cohort			
C	Consumption		μgC.d^{-1}	
ξ	Standard metabolism		μgC.d^{-1}	
G	Energy gain		μgC.d^{-1}	
m_T	Total mortality		d^{-1}	
m_p	Predation mortality rate		d^{-1}	
μ	Predation mortality rate at the surface		d^{-1}	
V_s	Search volume		L.d^{-1}	
C_m	Maximum consumption		μgC.d^{-1}	
f	Feeding level	[0,1]		
f_c	Critical feeding level	[0,1]		
e	Amount of food available relative to the maximum consumption	[0,1]		

Continued on next page

Table 5.1 – continued from previous page

	Description	Values	Units	References
τ_D	Fraction of daylight per day	[0,1]		
τ_s	Optimal time at the surface	[0,1]		
N_e	Number of eggs			
T_p	Date of the resource center of distribution		d	
w	Width of the resource		d	
Parameters				
a	Amplitude of the resource	8000	μgC.L^{-1}.d	
m_0	Background mortality	10^{-3}	d^{-1}	
α	Assimilation efficiency	0.6		Conover 1966
N_0	Initial number of individual in a cohort	10^5		
k_s	Metabolic cost relative to the weight	0.07	μgC$^{1/4}$.d^{-1}	
k_v	Search volume constant	$15.8 \cdot 10^{-3}$	μgC$^{-0.7}$.L.d^{-1}	Levinsen et al. 2000
k_c	Maximum consumption constant	1.68	μgC$^{0.3}$.d^{-1}	Saiz and Calbet 2007
k_m	Starvation mortality constant	5		
L	Latitude	70	degree	
c	Mortality constant	10^4	μgC$^{1/4}$.d^{-1}	
ν	Ratio surface/deep predation mortality rate	1/100		
Specific parameters for the size at maturity				
		Small Big		
W_e	Egg weight	0.191 0.56	μgC	Hygum et al. 2000, Conover 1967, Hirche 1989
W_a	Adult weight	92 940	μgC	Hirche and Kosobokova 2003

5.2.5 Population dynamics

If $m_T(w,t)$ is the total mortality (cf. section 5.2.4), the probability to be alive is:

$$\frac{\partial P}{\partial t} = -m_T(W,t)P(t) \tag{5.14}$$

The number of individuals in the cohort is found by multiplying the number of individuals N_0 when the cohort had been created with the probability to be alive P(t).

$$N(t) = N_0 P(t) \tag{5.15}$$

We delete the cohort following the rules listed in Appendix 5.B.

5.3 Results

5.3.1 Life-history dynamic in the model

Seasonality in food availability drives the copepod life history, influencing consumption, individual weight, time spend at the surface, and therefore survivorship and fitness (figure 5.1). At the beginning of their life, copepods suffer from a high mortality (predation mortality decreases with the size of the individuals), and in absence of food available, they suffer from starvation as soon as they finish the development time of their non feeding stage (panel i and j).

When the bloom starts, copepods should spend all their time at the surface (left side of the panel c and d) to maximize their feeding level (panel e and f) and therefore their growth. As soon as the food availability is getting more abundant, copepods is predicted to reduce their time at the surface strictly to the night-time when it is safe (panel c and d), decreasing thus their mortality (panel i and j). At first, the reduction of time spent at the surface decreases the feeding level, but it is soon compensated by the continuous food availability increase (panel e and f). Surplus of energy is assumed to be allocated entirely to the somatic pool (bold line, panel g and h), but as they grow, the metabolic cost also increases (thin line; panel e and f).

When the days are getting longer, and the time spend at the surface decreases following the night-duration, the feeding level is also declining. However, with the horizon of mid-night sun, copepods have to spend more time at the surface to cover their basic need and to compensate for a higher mortality rate due to their predation exposure during day-time (panel c and d). The feeding level is thus raising again (panel e and f), but so is the mortality (panel i and j).

The small income breeders reach their maturity size around the middle of the bloom (the bold curve reach a plateau, panel g) and start accumulating reserve (sharp pick of the thin line panel g). As soon as they have

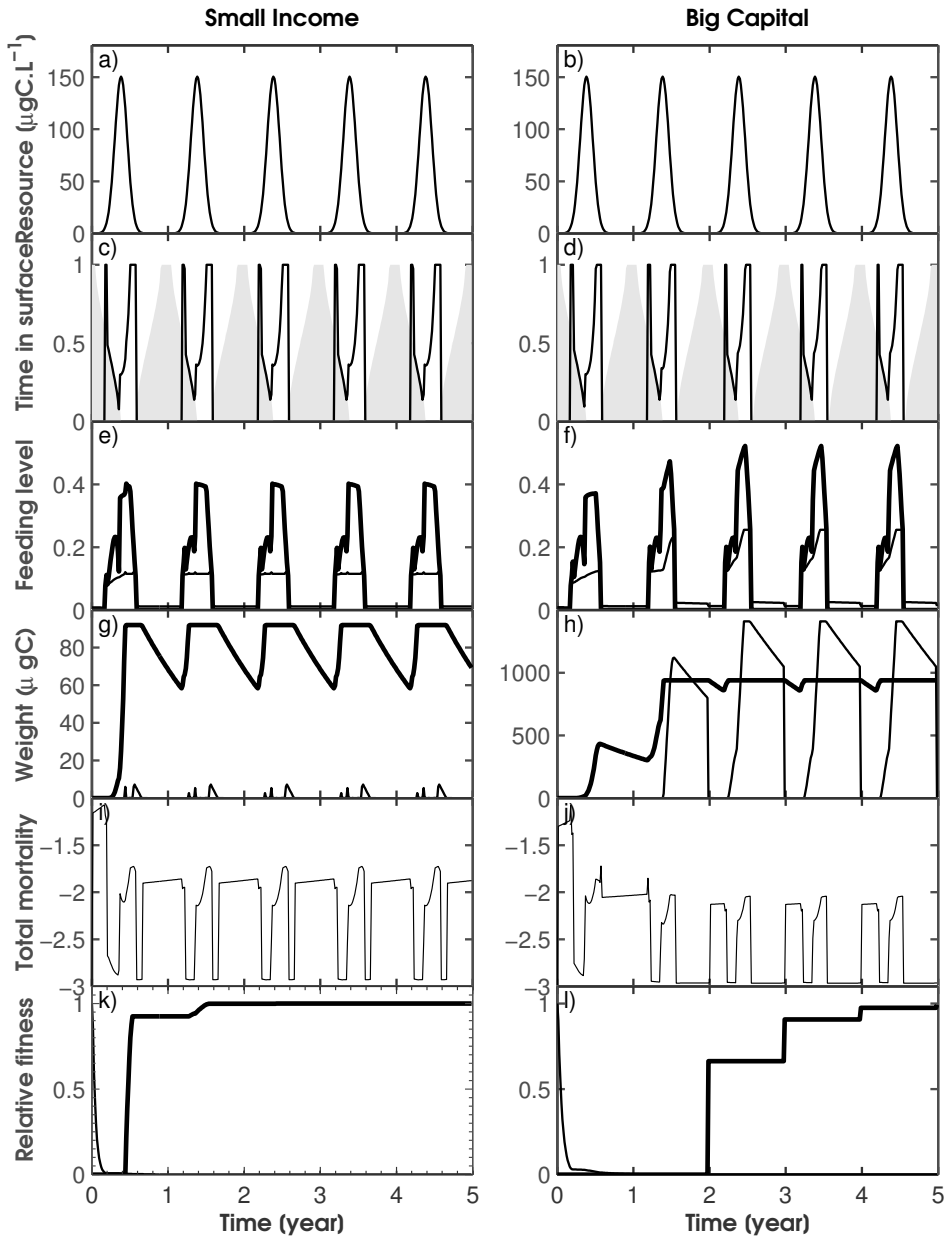


Figure 5.1: Cohort dynamic for a small income breeders (left) and for a large capital breeder (right). a-b) the resource available, c-d) the proportion of time spent at the surface (black line) and the fraction of night time per day (light gray), e-f) the feeding level (thick line) and the critical feeding level (thin line), g-h) the weight of the somatic (bold line) and reserves (thin line) pools, i-j) the total mortality in log scale, including the background, the predation and the starvation mortality, and in k-l) the relative fitness (number of offspring produced on the total number of offspring produced divided by the life time offspring production, thick line) and the probability of an individual in the cohort to be alive (thin line).

enough reserves to produce 50 eggs, income breeders start spawning and thus increase their relative life-time fitness (panel k).

When the bloom is depleting, copepods stay at the surface all day and night to maximize their growth, but their feeding level still decreases. Copepods find refuge at depth (panel c and d) and enter a diapause state (the metabolic cost is reduced; thin line panel e and f) as soon as the potential gain of energy, that they can acquire by feeding at the surface, becomes lower than the reduction of metabolic cost in diapause.

At the beginning of the following spring bloom, copepods rebuild their somatic pool until they reach their former maturity size, and then store reserves (panel g and h). The large size of capital breeders (right column) implies important metabolic cost (thin line, panel f) with the reserves pool reaching a maximum at 60% of the total weight (thin line panel h). In the winter, capital will rely on their reserves pool to cover metabolic cost, which induces a low mortality. At spawning time, the remaining reserves is assumed to be converted entirely to the egg production, implying that they dig into their somatic pool for the rest of the winter.

Because of this delay in spawning, capital breeders reach their life time fitness within 4 years, while the income breeders produce most of their offspring within a year, due to their fast development and high mortality. Hence, the income breeders reach a high fraction of their total offspring production early in their life time (start to spawn early but suffer from a high mortality), while the large capital breeders start spawning later in their life, but suffer from a lower mortality rate.

5.3.2 Capital breeders' best spawning time

An import factor driving the success of capital breeding is the spawning time: being able to spawn detached to the food available allows the capital breeders to spawn in a time which favor the fitness of their offspring (Varpe et al. 2007). Figure 5.2 explores the population growth rate of the two capital strategies as a function of their spawning time. The population maximizes its growth rate when spawning occurs prior to the spring bloom. Therefore, we consider in the model that the capital breeders lay their eggs before the spring bloom starts.

5.3.3 Income versus capital breeders and associated size at maturity

The four strategies is compared in relation to the spring bloom width - the zooplankton main environmental factor (figure 5.3). The shape of the spring bloom is also a good indicator of the latitude and is subject to climate change (Falk-Petersen et al. 2007, Leu et al. 2011, Wassmann 2011).

When the spring bloom is short, the income breeder's offspring do not

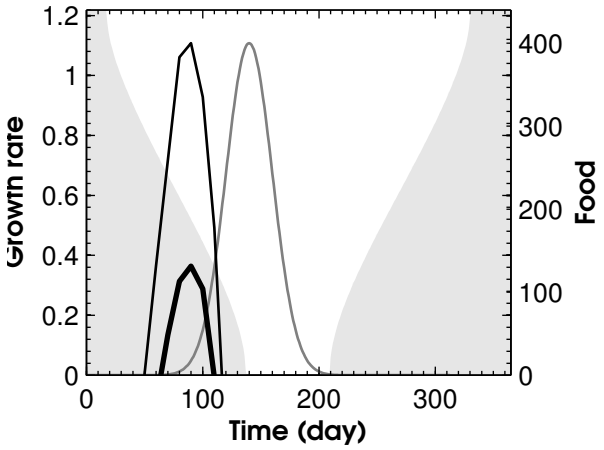


Figure 5.2: Population growth rate for a small capital (thin line) and a large capital (thick line) breeder as a function of the time of spawning relatively to the food availability (gray line) and the night-length (light gray). The width of the bloom is fixed at 20 days, while the peak of the bloom is at 140 julian day.

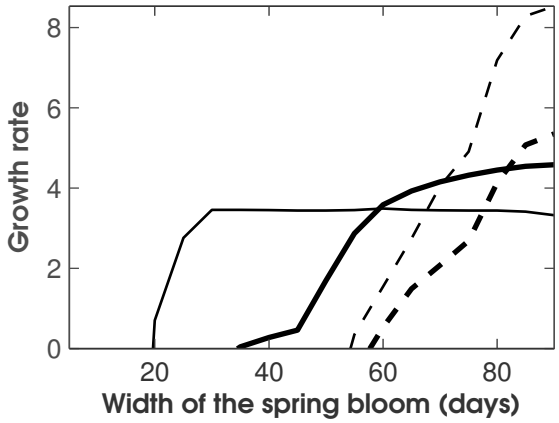


Figure 5.3: Population growth rate of the small income (thin dashed line), a large income (bold dashed line), a small capital (thin line) and a large capital (bold line) spawner as a function of the width of the spring bloom.

have enough time to grow at a suitable size to overwinter and therefore the population growth rate is negative. In the other hand, the capital breeders, which spawn before the bloom, allow their offspring to exploit the complete bloom duration. Oppositely, when the spring bloom is long, the income breeders perform globally better than the large capital breeders, as they have the potential to have more than one generation per year. Once the capital breeders reach their maximum storages (set to be 60% of their total

body mass), they still have to wait for the following year to spawn, and hence cannot take advantage of the remaining food availability. Storage capacity limits thus the capital breeder fitness in area where the bloom is long and productive.

5.4 Discussion

We have related the fitness of capital versus income breeders to a range of spring bloom width, while keeping the amount of nutrient constant in the system. The capital breeding is preferable when the spring bloom is short, while the income spawner seems to be the best strategy when the spring bloom is prolonged. These results are in correlation with the distribution of the two copepods in the Arctic. The copepods *C. hyperboreus* dominates the Arctic where the spring bloom is delayed and short, while the *C. finmarchicus* dominates the North Atlantic, where the spring bloom is longer (Falk-Petersen et al. 2007).

When looking at the best time for spawning, capital breeders were able to use the reserves freshly made, when the spawning time happens during the productive period. Therefore, we interpret capital breeding as a single spawning event per year, using the entire reserve pool, disregarding when these have been accumulated. In reality, the capital breeders *C. hyperboreus* spawn in the deep, therefore they are not able to eat just before spawning. We also assume that spawning happens in one day, while in reality the eggs laying is spread in time. A wide range of spawning time ensures that at least part of the offspring will match the spring bloom, especially in a context of inter-annual variation in the spring bloom timing, such as the Arctic ocean environment.

In the model, we do not consider density dependence, as we assume that the spring bloom is not depleted by the secondary producers but by lack of nutrient in the system. Furthermore, the overwintering decision is considered to be driven only by food availability. However, some studies suggested that the predation pressure can also push copepods to find refuge in the deep layer and enter diapause while the level of food at the surface is still high. Thus, vulnerable large capital breeders (i.e. full of reserves) are unlikely to spend all day long at the surface at the end of the bloom (Sainmont et al. prep) and are expected to find refuge in overwintering earlier.

A surprisingly result compared to the observations is the high population growth rate of the small capital breeders compared to the large ones. A large size at maturity has the advantage that they can store more reserves, and potentially spawn more the next year. However, a delay in reaching maturity size increases mortality rate, such as the benefit of large size is restricted to prolonged feeding season (i.e. individuals able to reach maximum size within

a year). In environment where the inter-annual variability in the timing of the bloom could push individual to be larger such as they would be more resilient to a delay in food availability. An argument in favors of the large size observed in the *C. hyperboreus* species inhabiting the Arctic Ocean.

In conclusion, we demonstrated the influence of the width of the spring bloom on the breeding trait selection in copepods. Capital breeding is selected in short feeding season, while income breeding is the best strategy in prolonged feeding season. It is better for the capital breeders to be as large as possible without delaying their maturation, although income breeding favors small maturity size.

Appendix

5.A Optimal foraging time

Zooplankton and small pelagic fish are known to perform DVM in order to avoid visual predators at the surface during daylight hours and forage on phytoplankton during night-time (a schematic representation of the DVM issue is represented in chapter 1 - figure 1.7). However, at high latitude and during midnight sun, DVM is still observed (Dale and Kaartvedt 2000), which suggest that the darkness is not the only parameter involved into this migration. Here we propose a general method to take into account the reduced foraging and predation mortality due to DVM.

To investigate the reduced foraging time and mortality as a function of latitude and time of the year, we search for the optimal time individuals should spend at the surface in order to optimize their fitness. Considering two habitats: the arena (the surface layer, with food but with high mortality μ), and a refuge (the deep, where there is no food but the predation mortality is reduced by a factor $\nu \ll 1$). Maximum fitness (F^*) is obtained with a myopic approach based on Gilliam's rule (Gilliam and Fraser 1987). We thus look at finding the best fraction of time spend at the surface (τ_s) which maximizes the ratio between the growth rate g and the predation mortality (m_p):

$$F^*(\tau) = \max_{0 \leq \tau_s \leq 1} \left[\frac{g}{m_p} \right] \tag{5.16}$$

where the growth rate is function of the feeding level (f, ratio between the consumption $C(t)$ and maximum consumption C_m), and the critical feeding level ($0 \leq fc \leq 1$, minimum consumption needed to cover the metabolic cost).

$$g = \alpha C_m (f - f_c) \tag{5.17}$$

$$f_c = \xi / \alpha C_m \tag{5.18}$$

The feeding level ($0 \leq f \leq 1$) is reduced with the time spend at the surface:

$$f = \frac{\tau V_s R}{\tau V_s R + C_m} \tag{5.19}$$

We choose this formulation as we consider that the feeding level is dominated by the digestive time rather than the search for food.

The predation mortality m_p is equal to the surface predation morality rate at the surface (μ) when individuals are at the surface during dangerous hour (during $\tau - (1 - \tau_D)$), and to a reduced predation mortality rate in presence of darkness at the surface ($1 - \tau_D$) and in the deep habitat ($1 - \tau$):

$$m_p = \mu[\tau - (1 - \tau_D) + (2 - \tau - \tau_D)\nu] \tag{5.20}$$

Therefore, the fitness function can be written as

$$F(\tau) = \frac{\alpha V_s R}{\mu}(\frac{\tau}{e\tau + 1} - \frac{f_c}{e})\frac{1}{\tau - (1 - \tau_D) + (1 - \tau)\nu} \tag{5.21}$$

where $e = \dfrac{V_s R}{C_m}$ is the amount of food available at the surface relative to the maximal consumption. The fitness reaches a maximum at τ^* ($0 \leq \tau^* \leq 1$):

$$\tau^* = \frac{f_c(1-\nu) + \sqrt{f_c(1-\nu)^2 + e(1-f_c)(1-\nu)[\nu - (1-\tau_D)(1-\nu)]}}{e(1-f_c)(1-\nu)} \tag{5.22}$$

We assumed that the copepods reduce their metabolic cost from a factor of 10 (diapause state) when there is low food at the surface. They remain in

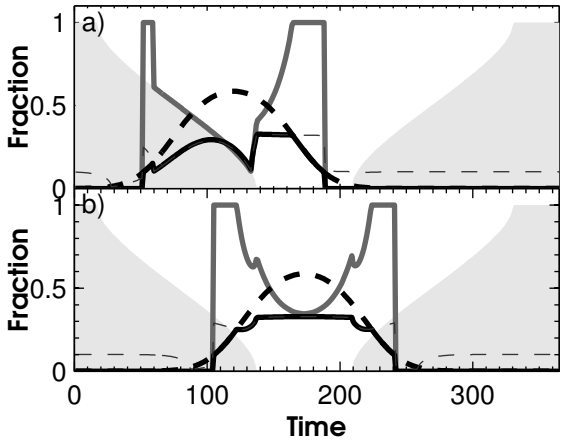


Figure 5.A.1: Optimal foraging time (thick gray line) of the copepods and the feeding level (thick black line) as a function of night-length (light gray) and the maximum feeding level reach if they spend all their time at the surface (bold dashed line). For references, the optimal feeding level are also represented in this graph (thin dashed line). The spring bloom peak is set for 120 Julian day on the left graph and for 173 Julian day (solstice) on the right graph. The width is 15 days and the simulation is run for an individual of $1000 \mu g C$.

diapause stage when the maximum surplus of energy from feeding ($\alpha C - \xi$) is below the reduced metabolic cost ($\xi/10$). τ_s is null in these circumstances.

$$\tau_s = \begin{cases} \max(\tau^*, 1 - \tau_D(t,l)) & \text{for } \alpha C - \xi < \xi/10 \\ 0 & \text{otherwise} \end{cases} \tag{5.23}$$

The result of this optimization is showed in figure 5.A.1.

5.B Diminution of the number of cohort

The cohort is deleted if the number of individuals in the cohort is below 1 ($N(t) < 1$). The number of cohort is reduced when it exceeds a high number (100 cohorts) with respect of the mass conservation.

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Chapter 6

Capital versus income breeder in a seasonal environment

Sainmont, J., Andersen, K. H., Varpe, Ø, and Visser, A. W. (Submitted). *American Naturalist*

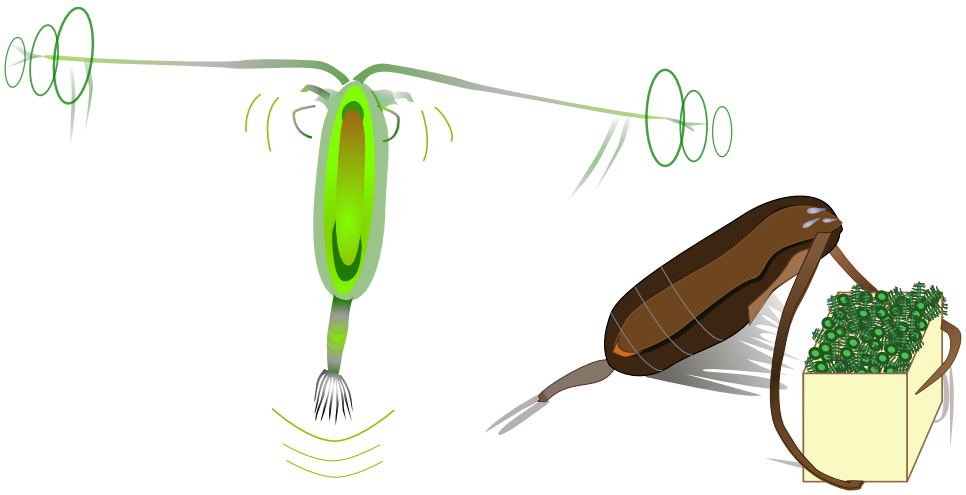

Fig: Parody of the Jean de la Fontaine fable "the grasshopper and the aunt"

Capital versus Income breeder in a seasonal environment

Abstract

The allocation of resources between growth, storage and reproduction is a key trade-off in the life history strategies of organisms. A central dichotomy is between capital breeders and income breeders. Capital breeders allocate resources to storage so as be able to reproduce independent of food availability, while income breeders allocate ingested food directly to reproduction. Motivated by copepod studies, we use an analytical model to compare the fitness of income against capital breeding in a deterministic seasonal environment. We analyze the fitness of breeding strategies as a function of feeding season duration and size at maturity. Small capital breeders perform better in short feeding seasons, but fall behind larger individuals when the length of the feeding season increases. Income breeding favors smaller individuals as they can have multiple generations within a year and thereby achieve a high annual growth rate, out-competing capital breeders in long feeding seasons. Therefore, we expect to find a dominance of small income breeders in temperate waters, while large capital breeders should dominate high latitudes where the spring is short and intense. This pattern is evident in nature, particularly in organisms with a generation time of a year or less.

Keywords: Income breeder, capital breeder, reproductive strategy, feeding season, spring bloom, life-history traits

6.1 Introduction

In seasonal environments, the timing of resource allocation to reproduction has direct consequences for fitness and for population dynamics. In general, an individual can either allocate available resources to reproduction directly (income breeder), or build up reserves while resources are available and reproduce at some future date (capital breeder; Drent and Daan 1980, Stearns 1992, Jönsson 1997). An individual can also adopt a mixed strategy, either by capital breeding followed by income breeding (Varpe et al. 2009), or by concurrent food intake added to storage before reproduction commences (Houston et al. 2007).

In constant (non-seasonal) environments, one can expect the income breeder to be the superior competitor as its strategy ensures the maximum rate of offspring production, with the possibility of multiple generations per year. However, this strategy becomes less effective when seasonality in resource availability and mortality risk shape the fitness of an individual as a function of its time of birth (Varpe et al. 2009, Ejsmond et al. 2010). For example for copepod species living in high latitude seas, adverse conditions during the winter ensure a strong selection on the state of individuals at the end of the feeding season, underlying the hypothesis that offspring born late in the feeding season have a low fitness due to a lack of time to reach a suitable size to survive the winter (Varpe et al. 2007).

In this respect, capital breeding has potential advantages; producing fewer offspring but each with a greater survivorship. Indeed, since reproduction is not directly related to the feeding season, capital breeders have the possibility to reproduce at a time and location that maximizes the fitness of their offspring (Jönsson 1997, Varpe et al. 2009). This strategy is however not without a risk, as in postponing reproduction until the following feeding season, the adult and its potential offspring may be killed before having a chance to be realized, illustratively referred to as a pre-breeding cost of reproduction (Jönsson 1997, Jönsson et al. 1998). Along with the income-capital trait, size (e.g. for copepods; size at maturity, or of eggs, or their ratio) is a key trait influencing fitness. In particular, adult size influences their ability to acquire resources, as well as their mortality and metabolic rates; egg size influences fecundity and relative size determines the time needed for offspring to grow to adulthood (Charnov 2001, Andersen et al. 2008), their survivorship through this period, their predation mortality at adult stage, and eventually their capacity to survive the winter. In seasonal environments, species have to cope with the restricted duration of the feeding season, and therefore have to time their maturation and their breeding strategy with it. Within this context, a defining question is: what is the best breeding strategy (i.e. capital versus income breeding) and maturity size as a function of the duration of the feeding season?

Copepod species of the genus *Calanus* found in the North Atlantic and

the Arctic, present a rich example of the diversity of reproduction strategies that similar species can adopt. Three dominant *Calanus* copepod species in these water display the full spectrum of resource allocation: *Calanus finmarchicus* is close to a pure income breeder, using concurrent food intake to produce eggs even when reserves left over from the winter are available for egg production; *Calanus hyperboreus* is a pure capital breeder, spawning in very deep waters during the winter by using its reserves accumulated during the previous spring bloom; while *Calanus glacialis* adopts a mixed strategy, storing some reserves to spawn before the spring bloom and using the incoming food to spawn during the bloom as well (Falk-Petersen et al. 2009, Conover 1988). These three copepods are quite different in size, with *C. hyperboreus* being much larger than the two others. Although they display the same life cycle (they go through 6 stages of nauplii, and 5 stages of copepodite before reaching adult), adopt similar strategies to avoid visual predation (diel vertical migration) and overwinter in the deep ocean, their centers of distribution differ: *C. finmarchicus* dominates the North Atlantic, *C. hyperboreus* the Arctic, and *C. glacialis* the continental shelf and the fjords (Conover 1988) of northern latitude.

Optimization models have highlighted the adaptive value of storage and capital breeding for our understanding of such within-species diversity and resulting state-dependent life histories (Varpe et al. 2009, Fiksen and Carlotti 1998). However, we expect variability in breeding strategies and size to have evolved in response to environmental conditions, including seasonality in food availability and predation risk, similar to the Pan-Arctic within-species diversity observed in *C. glacialis* (Daase et al. 2013). Studies highlighting the rationale behind income versus capital breeding strategies have focused on relative trade-offs (e.g. cost–benefit of carrying storage in ectotherm and endotherm species, Bonnet et al. 1998, Jönsson 1997; or on the pre- and post-breeding investment of the parents, Jönsson et al. 1998), rather than investigating how the environment shapes the success of these different breeding strategies within species and for closely related species. In a recent paper, Stephens et al. (ress) found that the index of capital breeding (extent to which females rely on the fasting strategy for offspring provisioning) for pinnipeds increases with stronger seasonality and a decreased predictability of the environment. Here, we pursue this line of investigation, and show that the duration of the feeding season alone can select for breeding strategy and preferable size at maturity also in organisms with short life span.

In this study, we analyze how the duration of the feeding season alone can 1) influence the success of capital versus income breeders and 2) and how the relative fitness of these strategies varies with size at maturity. The study is based on a simplified life history of marine copepod species in order to use the species complex and strategy space to obtain insight of general relevance for seasonal environments.

6.2 Methods

We model the net reproduction of an individual and its offspring over one annual cycle for an income and a capital breeder in order to determine which of the two strategies has the highest fitness under given environmental conditions. Our central focus for the environmental conditions is the length of the feeding season. Thus, the year is divided in two: the feeding season (spring) and the rest of the year (nominally termed winter) where no food is available. For each strategy we first determine a life-cycle "bottleneck"; a state (age, weight) which if not achieved by a particular date (e.g. transition from winter to spring conditions) in the annual cycle, will result in a negligible probability of survival.

The fitness of a given strategy is set by the number of replicates one year later of the same state as the starting individual which are directly descended from this individual. We term this the "annual fitness", and, all things being equal, will be identical to the annual population growth rate irrespective of what state-date combination is chosen.

For a capital breeder, spawning time is a clear bottleneck as it will spawn its entire production at a fixed time of the year. Hence we start the calculation with an egg born at time t_0, and follow its development, growth and survival through the feeding season, its accumulation of reserves and descent into diapause, and its overwintering survival at depth, to calculate the number of eggs it is able to produce a year later.Thus, the expected number of eggs produced at spawning time one year birth, sets the fitness (figure 6.1A).

For an income breeder, the bottleneck is the size that an individual has to reach at the onset of the winter. Failure to do so would leave the individual with a low probability to survive the winter. Assuming that this is maturity size, the calculation starts with an adult sized individual at the end of the feeding season, and its weight and survivorship are followed through the winter and the next feeding season. This individual (discounted by its overwinter survivorship) grows and reproduces, and the number of its surviving descendants which reach maturity at the end of the feeding season sets our measure of fitness. Note that the main advantage of income breeders here is the potential to have several generations per year. Even if the cycle measured for the two breeding strategies does not start with the same individual stage, the measures of fitness are nevertheless equivalent since we measure the full life cycle in both cases for the same annual environmental cycle.

6.2.1 Assumptions

Individual growth and mortality (μ) are allometrically related to body weight w. Maximum growth is $hw^{3/4}$ and modulated by available food (see table

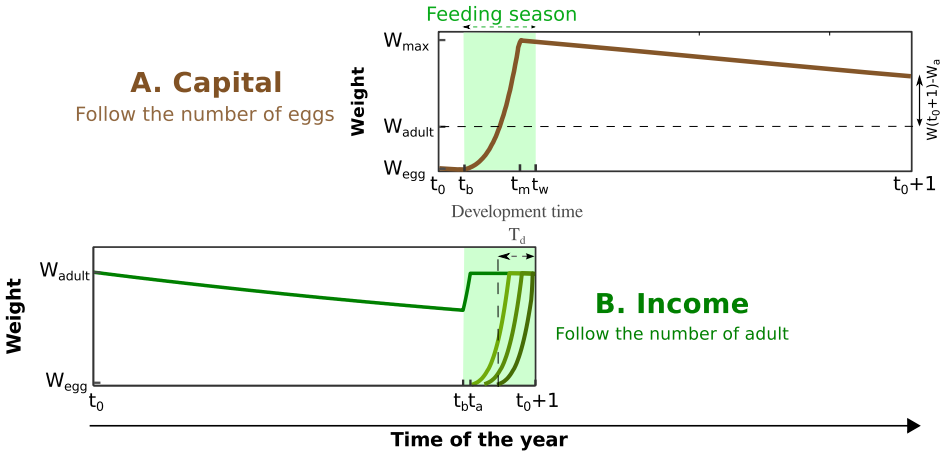

Figure 6.1: Weight of capital (A) and income (B) breeders. Capital breeders are born at time t_0, growing during the feeding season (gray area) until they reach maximum size (w_m) at t_m and enter dormancy until the end of the year (A). Income breeders start at adult size at the beginning of the winter (t_0), lose weight until the onset of the feeding season (t_b), after which they regain maturity at t_a. They spawn until the end of the feeding season, while their offspring reach the adult pool after their development time T_d (B). Additional generations are represented as shaded gray lines.

6.1 for parameter descriptions and values) to give :

$$\frac{\mathrm{d}w}{\mathrm{d}t} = h(f(t) - f_c)w^{3/4} \tag{6.1}$$

where h is the maximum consumption constant with units $\mu\mathrm{gC}^{1/4}\ \mathrm{d}^{-1}$. The seasonal variation in food is described by the non-dimensional feeding level $f(t)$ that denotes the fraction of maximum consumption which is available from the environment. $f(t)$ is modeled as box-car function:

$$f(t) = \begin{cases} 1 & t_b < t < t_w \\ 0 & \text{otherwise,} \end{cases} \tag{6.2}$$

where t_b and t_w mark the start and the end of the feeding season. The critical feeding level f_c denotes the fraction of maximum consumption $hw^{3/4}$ used for standard metabolism and activity.

Mortality is likewise assumed to follow allometric scaling with exponent $-1/4$ (Peterson and Wroblewski 1984, Hirst and Kiørboe 2002, Brown et al. 2004, Andersen and Beyer 2006):

$$\mu(w) = ahw^{-1/4} + \mu_0, \tag{6.3}$$

where μ_0 is a size-independent background mortality, and a is a non-dimensional constant characterizing the level of predation relative to the maximum con-

Table 6.1: List of symbols used.

Symbol	Description	Value	Units
w	Weight of an individual		μgC
$P_{t_1 \to t_2}$	Probability to survive from t_1 to t_2		
r	Annual fitness		ind·yr^{-1}
μ	Mortality rate		d^{-1}
w_a	Maturity weight		μgC
$f(t)$	Feeding level	[0,1]	
μ_a	Mortality rate at adult size	$ah_f w_a^{1/4} + \mu_0$	d^{-1}
θ	Reproductive investment		ind·yr^{-1}
Parameters:			
w_e	Egg weight	1	μgC
w_m	Maximum weight	$4w_a$	μgC
h_f	Factor for maximum consumption during the feeding season	1.01	μgC$^{1/4}$.d^{-1}
h_w	Factor for maximum consumption during the winter	0.10	μgC$^{1/4}$.d^{-1}
g_w	Reduction of h during winter	10	
μ_0	Size independent background mortality	10^{-3}	d^{-1}
ϵ_r	Conversion efficiency from adult to egg weight	0.5	
f_c	Critical feeding level	0.01	
a	Predation constant	0.1	

The units used are individuals (ind), microgram carbon (μgC), days (d) and year (yr).

sumption constant h. The presence of h in the predation mortality implies that increased growth (higher h) results in a higher mortality. This choice embodies a trade-off: faster growing individuals need to feed more and thereby face an increased risk of predation. On the other hand declining mortality with size (the $w^{-1/4}$ term) means that faster growing individuals lower their mortality through their faster increase in size. This trade-off is a formulation of the classic "M/K" life-history invariant (Charnov 1993) for a size-dependent predation mortality and furthermore a consequence size-spectrum theory, where consumption by predators is linked to the mortality of their prey (Andersen and Beyer 2006). The formulation of growth and mortality has the advantage that all parameters are non-dimensional except the consumption constant h.

The consumption constant is lowered by a non-dimensional factor g_w

between the feeding season (h_f) and winter (h_w) to reflect the decrease in metabolic costs and predation mortality during overwintering.

6.2.2 Elements of fitness

Calculating annual fitness requires that the weight $w(t)$ and survival $P(t)$ of an individual is known. The increase in weight Δw during a time interval t_1 to t_2 can be calculated by solving equation 6.1:

$$\Delta w_{t_1 \to t_2} = w(t_2) - w(t_1) = \left(\frac{h(f(t) - f_c)}{4} (t_2 - t_1) + w(t_1)^{1/4} \right)^4 - w(t_1) \tag{6.4}$$

The 4^{th} power of the term in the parentheses is needed to maintain the dimensions of weight of the term, and comes from the integration of equation 6.1.

Survival is determined partly by the declining mortality with size (eq. 6.3) and partly by the increase in weight (eq. 6.1). The survival during a time interval is found by solving $\mathrm{d}P/\mathrm{d}t = -\mu(w(t))P$:

$$P_{t_1 \to t_2} = \left(\frac{w(t_1)}{w(t_2)} \right)^{a/(f(t)-f_c)} e^{-\mu_0 (t_2 - t_1)} \tag{6.5}$$

From these two elements the annual fitness can be calculated as $r = P_{t_0 \to t_0+1} \theta$ where θ is the adult reproductive investment (time is measured in years, figure 6.1A). The time intervals used in the fitness calculation in both strategies are listed in table 6.2, while the probabilities to be alive and the individual weights are listed in table 6.3. All the equations follow directly from equation 6.4 and 6.5. Each strategy has its own quirks that need to be taken into account when the adult reproductive investment is calculated.

6.2.3 Capital breeder

Capital breeders grow and accumulate reserves during the feeding season to be able to spawn during the winter, prior to the next feeding season. We thus follow the development of an egg born at time t_0, with a weight w_e and investigate the number of offspring produced at the same date the following year $t_0 + 1$. During the feeding season individuals grow until they either reach their maximum size w_m (at time t_m) or they reach the end of the feeding season at time t_w. In either event, the adults enter dormancy and are subject to the winter conditions until spawning time at $t_0 + 1$.

In the fitness calculation it is important to distinguish between three cases: 1) individuals have a weight lower than maturity size w_a at spawning time, i.e. $w(t_0 + 1) < w_a$. This can happen if the individuals do not have time to mature during the feeding season ($w(t_w) < w_a$) or if the loss of

Table 6.2: Time interval as a function of individual characteristics.

Time interval	Value	Description
Capital		
$t_b \to t_w$	$4\frac{w_a^{1/4} - w_e^{1/4} + h_w f_c}{h_w f_c + h_f(1-fc)}$	Minimum feeding season duration to be larger that the maturity size at the end of the year
$t_b \to t_m$	$\frac{4(w_m^{1/4} - w_e^{1/4}) + h_w f_c(t_b - t_0)}{h_f(1-f_c)}$	Time to reach maturity size
Income		
T_d	$4\frac{w_a^{1/4} - w_e^{1/4}}{h_f(1-f_c)}$	Development time
$t_b \to t_a$	$\frac{h_w f_c}{h_f(1-f_c)}(t_b - t_0)$	Time to regain maturity size after the winter

weight during the winter is so large that the individual loses all its spawning capital (the interval $t_b \to t_w$ is shorter than the value from table 6.2); 2) individuals do not reach maximum size during the feeding season but are still able to spawn, i.e. $w_a < w(t_w) < w_m$; 3) individuals reach maximum size and enter dormancy during the feeding season ($t_b \to t_m < t_b \to t_w$):

$$r = \begin{cases} 0 & \text{case 1} \\ P_{t_0 \to t_b} P_{t_b \to t_w} P_{t_w \to t_0+1} \theta & \text{case 2} \\ P_{t_0 \to t_b} P_{t_b \to t_m} P_{t_m \to t_0+1} \theta & \text{case 3} \end{cases} \tag{6.6}$$

where the reproductive investment is:

$$\theta = \epsilon_r \frac{w(t_0+1) - w_a}{w_e} \tag{6.7}$$

and where ϵ_r is the reproductive efficiency and w_e is the weight of an egg.

6.2.4 Income breeder

The fitness calculation for income breeders is slightly more involved because not only do individuals reproduce throughout the feeding season, but they may also have multiple generations per year (figure 6.1B). For the income breeders, we follow the number of new adults over a year starting from the end of the feeding season. Two cases can be discerned depending on the duration of the feeding size: 1) individuals are unable to reach maturity

Table 6.3: Equations for weight and probability to be alive.

Time interval	Weight at the end of the interval	Probability to survive the interval
Capital		
$t_0 \to t_b$	$\left(-\frac{h_w f_c}{4}(t_b - t_0) + w_e^{1/4}\right)^4$	$\left(\frac{w_e}{w(t_b)}\right)^{-a/f_c} e^{-\mu_0(t_b - t_0)}$
Case 2:		
$t_b \to t_w$	$\left(\frac{h_f(1-f_c)}{4}(t_w - t_b) + w(t_b)^{1/4}\right)^4$	$\left(\frac{w(t_b)}{w(t_w)}\right)^{a/(1-f_c)} e^{-\mu_0(t_w - t_b)}$
$t_w \to t_0 + 1$	$\left(-\frac{h_w f_c}{4}(t_0 + 1 - t_w) + w(t_w)^{1/4}\right)^4$	$\left(\frac{w(t_w)}{w(t_0+1)}\right)^{-a/f_c} e^{-\mu_0(t_0+1-t_w)}$
Case 3:		
$t_b \to t_m$	w_m	$\left(\frac{w(t_b)}{w_m}\right)^{a/(1-f_c)} e^{-\mu_0(t_m - t_b)}$
$t_m \to t_0 + 1$	$\left(-\frac{h_w f_c}{4}(t_0 + 1 - t_m) + w_m^{1/4}\right)^4$	$\left(\frac{w_m}{w(t_0+1)}\right)^{-a/f_c} e^{-\mu_0(t_0+1-t_m)}$
Income		
$t_0 \to t_b$	$\left(-\frac{h_w f_c}{4}(t_b - t_0) + w_a^{1/4}\right)^4$	$\left(\frac{w_a}{w(t_b)}\right)^{-a/f_c} e^{-\mu_0(t_b - t_0)}$
$t_b \to t_a$	w_a	$\left(\frac{w(t_b)}{w_a}\right)^{a/(1-f_c)} e^{-\mu_0(t_a - t_b)}$
T_d	w_a	$\left(\frac{w_e}{w_a}\right)^{a/(1-f_c)} e^{-\mu_0 T_d}$
$t_a \to t_a + T_d$	w_a	$e^{-\mu_a T_d}$

during the feeding season or they do but their offspring do not have time to reach adult stage, i.e. ($w(t_0 + 1) < w_a$ or $t_b \to t_w < t_b \to t_a + T_d$, with T_d the development time from egg to adult); 2) one or several generations of offspring reach adult stage before the end of the feeding season:

$$r = \begin{cases} 0 & \text{case 1} \\ P_{t_0 \to t_b} P_{t_b \to t_a} P_{t_a \to t_a + T_d} \theta & \text{case 2} \end{cases} \tag{6.8}$$

In case 2, θ represents the rate at which adults are recruited to the population from successive generations founded by our focal animals. The rate of egg production and their probability to reach maturity during the feeding season of a single generation (r_p) is a function of the adult energy gain ($h_f(1 - f_c)w_a^{3/4}$), the conversion efficiency to egg production (ϵ_r), the egg

weight (w_e), and of the probability for an egg to grow to adult size (P_{T_d}):

$$r_p = P_{T_d}\epsilon_r \frac{h_f(1-f_c)w_a^{3/4}}{w_e} \tag{6.9}$$

The number of adults follows a delay differential equation of the form:

$$\frac{\mathrm{d}N(t)}{\mathrm{d}t} = -\mu_a N(t) + r_p N(t-T_d) \tag{6.10}$$

with the first term on the right hand side representing the mortality of the current adults, and the second term the recruitment of offspring born a time T_d earlier and having now reached adult size with survival probability P_{T_d}. μ_a denotes adult mortality rate at constant adult size ($\mu_a = \mu(w_a)$). θ is then:

$$\theta = \int_{t_a+T_d}^{t_0+1} \frac{\mathrm{d}N(t)}{\mathrm{d}t} dt \tag{6.11}$$

As the food availability is constant during the feeding season, the number of adults at time $t - T_d$ is a constant proportion of the number of adults at time t: $N(t-T_d) = \lambda N(t)$, with λ a constant (details in Appendix 6.A: Delay equation).

$$\lambda = \frac{W(r_p T_d e^{\mu_a T_d})}{T_d r_p} \tag{6.12}$$

The adult reproductive rate for the income breeder can then be written as:

$$\theta = \exp\left[\left(\frac{W(r_p T_d e^{\mu_a T_d})}{T_d} - \mu_a\right)(t_0 + 1 - t_a - T_d)\right] \tag{6.13}$$

with W is the Lambert function.

6.3 Results

In a very short feeding season, neither of the two reproduction strategies can maintain a positive growth rate within an annual cycle (figure 6.1). When the feeding season gets longer, small capital breeders have the highest annual fitness first, but are soon overtaken by the larger capital breeders. This is due to storage capacity, which is a constant fraction of maturity size (cf. with bigger storage capacity, larger capital breeders profit from a longer feeding season). It is thus advantageous for a capital breeder to be as large as the length of the feeding season allows. The optimal maximum size, given a feeding season duration is:

$$w_m^* = \left(\frac{h_f(t_w - t_b)(1-f_c) - h_w f_c(t_b - t_0)}{4} + w_e^{1/4}\right)^4 \tag{6.14}$$

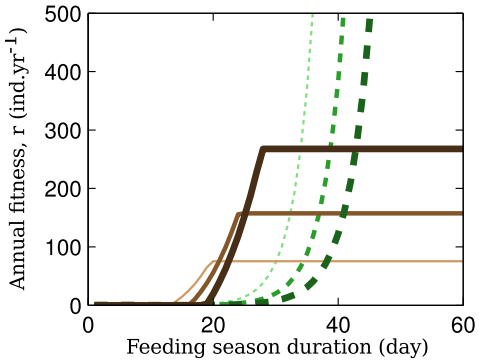

Figure 6.1: Fitness of capital (solid) and income breeders (dashed) for three different weights at maturity (thin line, $w_a = 300$ μgC; medium line, $w_a = 600$ μgC; and thick line, $w_a = 1000$ μgC).

As the length of the feeding season increases it becomes long enough to allow the income breeders to have several generations per season, leading to an exponential increase in their fitness. Eventually when the feeding season becomes sufficiently long, income breeders start to out-compete capital breeders. The length of the feeding season where this cross-over occurs is a complicated function of the parameters (Appendix 6.B: From capital to income breeding). Small income breeders out-compete larger ones as they reach maturity size faster and therefore can contribute more rapidly to the next generation and eventually have the opportunity to have a higher number of generations within a year. Therefore the cross-over between the capital and income strategies happens between large capital breeders and small income breeders. For the current parameters this occur at a length of the feeding season around 30 days.

Sensitivity analyses on the main parameters used in this study reveal that the pattern of dominance by large capital breeders during short seasons and small income breeders during long seasons is quite robust (figure 6.2). An increment in the critical feeding level increases the need of all the strategies for a longer feeding season (figure 6.2D). The large maturity size, by having a relatively lower predation mortality compared to smaller individuals, are less affected by an increase in predation constant. Large capital breeders thus dominate over small income breeders through a longer window of feeding season duration (figure 6.2E).

6.4 Discussion

We have demonstrated the relative benefit of the two pure reproduction strategies as a function of the feeding season duration, and highlight that size at maturity also plays an important role in the reproduction success. Capital

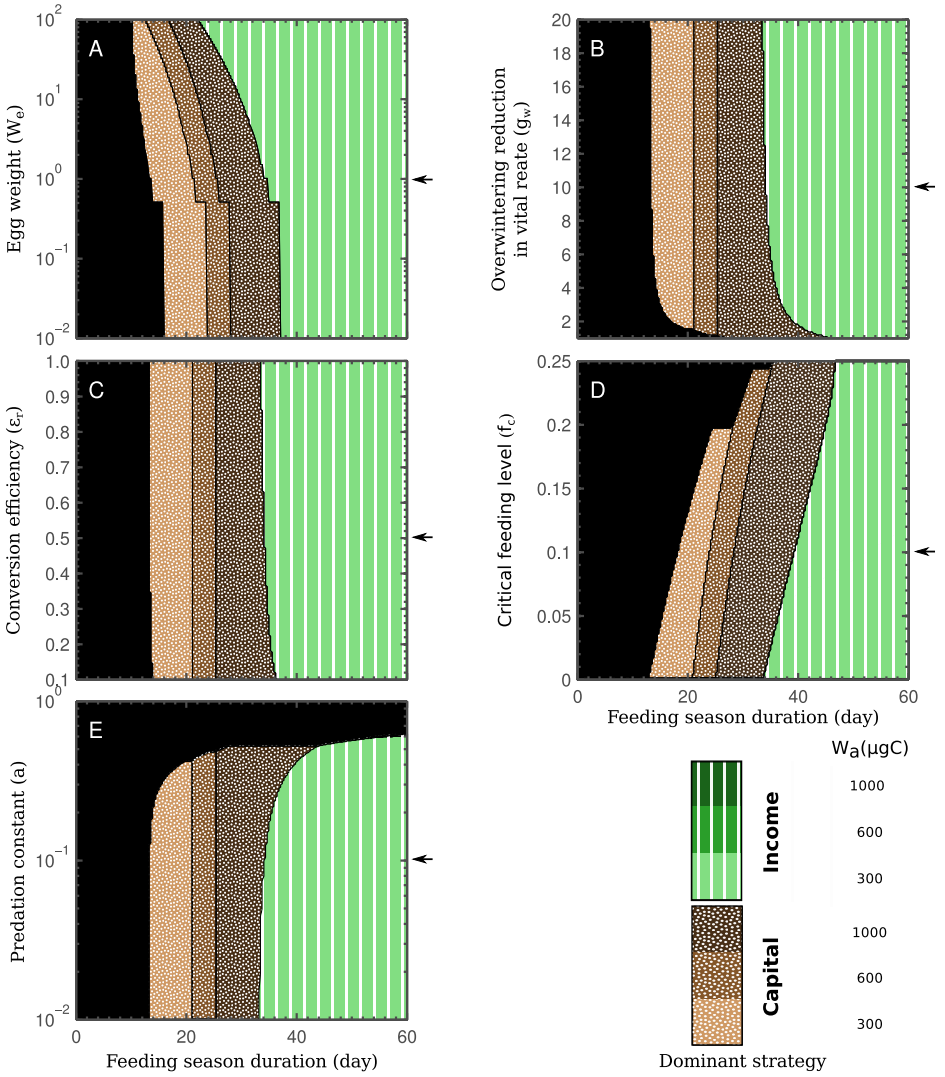

Figure 6.2: Dominance succession of income (vertical stripes pattern) and capital breeding (dots pattern) with different size at maturity (light gray, $w_a = 300\mu$gC; medium gray, $w_a = 600\mu$gC; and dark gray, $w_a = 1000\mu$gC), for a variation in the egg weight (w_e, A), in overwintering reduction in vital rate (g_w, B), in conversion efficiency from individual weight to eggs weight (ϵ_r, C), in critical feeding level (f_c, D), and in predation constant (a, E). Black areas indicate that all the strategies have zero fitness; the arrows indicate the values used in figure 6.1.

breeders should be as large as possible to support a maximum amount of reserves (supporting the speculation by Jönsson 1997) and generally perform well in short feeding seasons, while income breeders should be as small as possible to allow multiple generations within a year and take advantage of long feeding seasons.

Following this pattern, large capital breeders should be found at high latitude, while income breeders should dominate temperate waters. This is the case for the *Calanus* copepods in the Atlantic and the Arctic: large *C. hyperboreus* dominate the Arctic, by spawning prior to the phytoplankton bloom in deep water (capital breeding), while *C. finmarchicus*, somewhat smaller and breeding mostly based on incoming food resources, dominate the North Atlantic where the phytoplankton bloom is longer (Conover 1988). Similarly, the copepods in the North Pacific follow the same pattern with the capital breeder *Neocalanus* spp. dominating the area with short blooms while the smaller income breeder *Eucalanus* spp. has a southern distribution and is successful in the Eastern gyre Pacific where the feeding season is prolonged due to local physical conditions (Miller et al. 1984, Tsuda et al. 2004). Further comparisons to other taxa require that individuals have the capacity to store reserves, to retreat in overwintering, and to have the possibility for multi-generations within a feeding season. For example, mysids fulfill the conditions. In the genus *Mysidopsis* and *Erythrops*, the species *M. didelphys* and *E. erythrophthalma*, both capital breeders (Tattersall 1969, Mauchline 1970, Buhl-Jensen and Fosså 1991) are found in higher latitudes of the North Atlantic than their smaller conspecifics of the same genus *M. gobbosa*, *M. angusta*, *E. elegans* and *E. serrata* (Mauchline 1968; 1971).

Although many fish species are longer lived than 1 year, latitudinal gradients seems to select for the breeding strategy type. McBride et al. (2013) analyzed the reproduction strategy of fish with an indication of the habitat they live in. From this review, a clear latitudinal gradient can be made with fish present in the temperate and subtropical area being mostly income breeders (e.g. the Inland silverside *Menidia beryllina* or the bay anchovy *Anchoa mitchilly*), while the species inhabiting the boreal latitudes are all capital breeders (e.g. the Atlantic and Pacific herring *Clupea harengus* and *C. pallasii*, haddock *Melanogrammus aeglefinus* and the sea lamprey *Petromyzon marinus*). In temperate waters, both income and capital breeders are found (e.g. three-spined stickleback *Gasterosteus aculeatus* is an income breeders while the white crappie *Pomoxis annularis* is a capital breeder), and mixed strategy are common (e.g. european sprat *sprattus sprattus*, northern anchovy *Engraulis mordax* or European sea bass *Dicentrarchus labrax*). However, this pattern is not without exception, with for example the Spiny chromis *Acanthochromis poluacanthus*, living in a tropical environment is a capital breeder, and cross latitudinal distributed species being either income (e.g. Mummichog *Fundulus heteroclitus*) or capital breeders (e.g. Brown trout *Salmo trutta*). Comparison within genus is

sometime possible, such as the sand sole *Solea solea*, a capital breeder found up to Trondheim Fjord, while its close relations *Solea lascaris* and *Solea impar* are income breeders, with northern limits in the southern North Sea and along the Brittany coast respectively. Comparisons with larger species would however be more difficult, as long gestation and parental care, are expected to play an important role into the breeding strategy pay-off.

In this study, we have focused on the two pure reproduction strategies. However, there is a distinct possibility that mixed strategies can at times be superior. Based solely on the requirements of gathering sufficient reserves, capital breeders go into diapause before the end of the feeding season. They could however use the remainder of the feeding season to switch to an income breeding mode. While this may increase reproduction, the downsides are an increase in mortality and the possibility that their offspring will not reach a suitable stage before winter sets in. It is therefore beneficial to switch to income breeding if the remainder of the feeding season is longer that the development time and increased mortality is limited. Capital breeders could also target a multiyear cycle, which could allow them to maintain a positive growth rate in shorter feeding season. This is a strategy adopted by the largest of the *Calanus* cousins, *C. hyperboreus* (Conover 1988, Swalethorp et al. 2011). On the income breeders side, offspring could go into diapause as soon as they reach adult size, investing in survivorship for the next year instead of gambling on a next generation which may not reach a suitable size to overwinter (Kaartvedt 2000). Income breeder's offspring could also store some reserves, and conduct a degree of capital breeding before the feeding season, and still spawn during the next feeding season relying on food availability as seen with *C. glacialis* (Hirche and Kattner 1993, Daase et al. 2013).

The pattern of success for income and capital breeders presented here, and the speculation on mixed strategies, relies on mortality decreasing with individual size. This allometric relationship is a general trend observed amongst organisms throughout the marine pelagic environment (Peterson and Wroblewski 1984, Hirst and Kiørboe 2002). This allows us to find analytic solutions to our problem. However, it has been argued that mortality could increase with stage among *Calanus* species (Eiane et al. 2002), especially in the presence of visual predators (Aksnes and Giske 1993). Higher mortality at larger size could induce smaller maturity size, or the emergence of predation avoidance strategies such as diel vertical migration (Lampert 1989, Ohman 1990, Sainmont et al. 2013), or a switch in feeding mode (ambush, cruise or filter feeding; Kiørboe et al. 1996, Visser and Fiksen 2013).

Predation mortality can also vary with seasons, with for example an increase of predation pressure toward the end of the phytoplankton bloom with the increase in predator abundance (e.g. fish larvae), through seasonal presence of migrating fish predators (Kaartvedt 2000), or seasonal change in the performance of visually searching predators (Varpe and Fiksen 2010). In

this situation a mixed strategy could be beneficial and push individuals to find refuge while food is still available at the surface. This earlier overwintering balances a reduction in capital breeding energy storage over an increase in survivorship. Income breeder offspring could also have an advantage to overwinter as soon as they reach a suitable size instead of engaging another generation. Capturing another mortality dynamic, either another allometric relationship or an intra-annual variation would set an extra level of complexity into the mathematical calculations, and are therefore not treated in this study.

Here we have addressed a variable but predictable environment. In nature, interannual uncertainty is likely to affect the long term success of a population and could be calculated as the geometric mean of the successive year fitness (Yoshimura and Clark 1991, McNamara et al. 1995). Under the condition that capital breeders do not miss the feeding season, spawning prior to the spring bloom seems to be a robust strategy. To give the best chance to their offspring, capital breeders should spawn early in the year and provide enough energy storage to their offspring so they can wait for the beginning of the feeding season (Varpe et al. 2007). Capital breeders should thus choose fewer larger offspring over a large number of smaller offspring (Stearns 1976, Doughty and Shine 1997, Yoshimura and Clark 1991). Further, adults could spread their reproduction in time to increase the chances that, at least some of their offspring survive to the feeding season.

On the other hand, income breeding strategy seems to be quite risky in an uncertain environment, as a bad year, or a long winter could lead to extinction. Furthermore, animals should be larger than in a predictable environment, as they are more resilient to long winters and to a delay in food availability (Real and Caraco 1986). Interannual uncertainty and long winters could thus explain the size differences between similar animals adopting the same strategies (as suggested in a copepod study in the subarctic Pacific; Mackas and Tsuda 1999). For example, *C. finmarchicus* is found in higher latitude in the Atlantic than its smaller cousin *Calanus helgolandicus* (Planque and Fromentin 1996), although they both adopt an income breeding strategy (Conover 1988). Thus, larger size at birth and at maturity, along with strategy diversification could be a response of species to uncertain environments.

Our calculation is based on the absence of feedback from the environment (density dependence) and competition between income and capital breeders at different sizes (frequency dependence). Depending on how density dependence and frequency dependence operate, the fitness calculations could be more or less correct (Mylius and Diekmann 1995). Specifically, while the absolute value of our fitness estimate may be considerably off, we may expect the relative ranking of the various strategies to remain invariant to density dependent effects. Simulations of competing populations with explicit density-dependence would be needed to rigorously address this issue.

However, because of the robustness of the results and the intuitive understanding we have developed, we do not expect the general conclusions to be compromised.

In conclusion, we demonstrated the succession of the capital followed by income breeder traits when the feeding season duration increases. Capital breeders should be as large as they can reach during the feeding season, while income breeder should remain small.

Acknowledgements

We wish to thank the associate editors Dr. Sean H. Rice and the two anonymous reviewers for their constructive and fruitful comments. Their time and efforts improved the paper substantially. This work was supported by the Greenland Climate Research Centre and the Centre for Ocean Life, a VKR center of excellence supported by the Villum foundation. Øystein Varpe was supported by the Research Council of Norway through the project Arctic Production - 227046/E10.

Appendix

6.A Delay equation

We look for a closed form for equation 6.15

$$\frac{dy}{dt} = ry(t-b) - \alpha y(t) \tag{6.15}$$

with α, b and r being some constants. We approximate this equation by assuming that the number of adult at time $y(t-b)$ is a fraction of the population at time $y(t)$:

$$y(t-b) = \lambda y(t) \tag{6.16}$$

Therefore, equation 6.10 can be written as:

$$\frac{dy}{dt} = (\lambda r - \alpha)y(t) \tag{6.17}$$

we therefore have:

$$y(t) = y(0)e^{(\lambda r-\alpha)t} \tag{6.18}$$

Similarly

$$\begin{cases} y(t-b) & = y(0)e^{(\lambda r-\alpha)(t-b)} \\ & = y(t)e^{-(\lambda r-\alpha)b} \end{cases} \tag{6.19}$$

Or by definition $y(t-b) = \lambda y(t)$, λ is therefore the solution to

$$\lambda = e^{-b(\lambda r-\alpha)} \tag{6.20}$$

With $W(z)$ the lambert function, solution of the equation $z = W(z)e^{W(z)}$, we have

$$\lambda = \frac{W(bre^{\alpha b})}{br} \tag{6.21}$$

The solution of equation 6.10 is therefore :

$$y(t) = y(0)\exp\left(\left(\frac{W(bre^{\alpha b})}{b} - \alpha\right)t\right) \tag{6.22}$$

6.B From capital to income breeding

For capital and income breeders of the same size, their fitness become equivalent when the feeding season duration is:

$$\Omega = 1 - \frac{4}{h_w f_c}(w_a^{1/4} - e^{\beta-\sigma}); \tag{6.23}$$

with β, and σ:

$$\beta = \frac{1-f_c}{4ah_w}\left(4(\mu_0+\theta_p)(\xi+1)w_a^{1/4} - h_w f_c\left(\theta_p(\xi+1) - \ln\left(\frac{r}{K}\right)\right)\right) \tag{6.24}$$

$$\sigma = W\left(\frac{(\mu_0+\theta_p)(\xi+1)(1-f_c)}{ah_w}e^{\beta}\right); \tag{6.25}$$

along with ξ, θ_p and K :

$$\xi = \frac{h_w f_c}{h_f(1-fc)} \tag{6.26}$$

$$\theta_p = \frac{W(r_p T_d e^{\mu_a T_d})}{T_d} - \mu_a \tag{6.27}$$

$$K = w_a^{\frac{-a}{fc(1-fc)}} e^{-\mu_a T_d - \theta_p(\xi+T_d)} \tag{6.28}$$

r is the fitness of the capital breeder where they reach maximum size during the feeding season (case 3).
For feeding season durations less than this, capital breeding is superior to income breeding.

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